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Foraging ecology of male Cerulean Warblers and other Neotropical migrants

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ABSTRACT

Foraging ecology of Neotropical migrants, with concentration on male Cerulean Warblers

Gregory A. George

Understanding foraging ecology provides insight into species resource requirements and overall conservation needs. We examined foraging behavior and tree species selection of male Cerulean Warblers (*Dendroica cerulea*) (n = 673) in response to varying degrees of habitat disturbance from silvicultural treatments at four study sites in West Virginia, Kentucky and Ohio, during the 2006 and 2007 breeding seasons. Cerulean Warblers foraged primarily in the forest canopy, along branch tips by gleaning insects off leaf surfaces, often adjacent to canopy gaps, both pre- and post-harvest. Tree species availability, based on importance values (IV) calculated from density, frequency and basal areas, differed from tree species used for foraging both pre- and post-harvest ($p<0.01$). Preferred species included hickory (*Carya spp*.), sugar maple (*Acer saccharum*), and chestnut oak (*Quercus prinus*), although red oak (*Quercus rubra*) was strongly avoided. Tree species selection changed little post-harvest in all silvicultural treatments. Aerial foraging increased after harvests. Cerulean Warblers exhibited selection preferences, suggesting, maintaining availability of preferred tree species is important for management of Cerulean Warbler populations.

Species resource requirements are an important component of habitat selection. We investigated foraging ecology and tree species selection of five Neotropical migrant species (n = 679); American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Hooded Warbler (*Wilsonia citrine*), Red-eyed Vireo (*Vireo olivaceus*), and Scarlet Tanager (*Piranga olivacea*) at three study sites in West Virginia during breeding seasons of 2006 and 2007. We analyzed influences of habitat disturbance from silvicultural treatments implemented during the non-breeding season between years. Tree species availability, based on importance values (IV) calculated from relative density, frequency, and basal area, differed from tree species used for foraging pre and post-treatment. Species varied in their preferred maneuver types and degree of tree species selectivity. Aerial maneuvers increased post-treatment for all species except Black-and-white Warblers. At the guild level, sugar maples were preferred and red oaks were avoided. Tree species selection changed little post-harvest. Red-eyed Vireos and post-harvest American Redstarts exhibited significant tree species selection preferences ($P < 0.05$) although Scarlet Tanagers were near-significant in tree species selection ($P = 0.06$).

Foraging ecology studies could be biased due to disparity in initial detection probabilities of foraging birds among tree species or foraging behaviors because it might be easier to detect a foraging bird when it is in certain tree species, lower in the canopy, or using aerial foraging maneuvers. Our study investigated whether the initial foraging observation is biased based on 1521 paired, single-point foraging observations for six species of arboreal foraging Neotropical migrants in two study sites in West Virginia and one in Kentucky in 2006 and 2007. We did not detect a significant difference in tree species used for foraging between the initial and second foraging observation ($P \geq 0.62$). Foraging maneuvers and foraging height generally were not significantly different ($P \geq 0.09$) between the two foraging observations for the six avian species tested. We conclude that the initial detection of foraging birds would not have a major influence on interpretation of foraging substrate or behavioral preferences.

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CHAPTER 1

INTRODUCTION

Cerulean Warblers (*Dendroica cerulea*), once common, have declined at a net rate of 4.1% per year from 1966 through 2007 (Sauer et al. 2008). Although they have recently expanded in parts of their range, the species appears to be declining primarily in the core of their breeding range (Jones et al. 2004, Sauer et al. 2008). Partners in Flight has ranked the Cerulean Warbler second overall, in the Northeast region, for species warranting immediate conservation action (Rosenberg and Wells 2000). Consequently, Cerulean Warblers are a focal species for conservation efforts (Hamel et al. 2004).

Life history information on the Cerulean Warbler is limited, particularly as it pertains to foraging ecology. Yet, understanding foraging behavior can provide insight into the ecology of Neotropical migrants and can shed additional light on their requirements and thus on their overall conservation needs (Petit et al. 1995). Rosenberg et al. (2000) found regular use of multiple tree species in West Virginia for foraging and singing by the Cerulean Warbler such as Chestnut Oak (*Quercus prinus*), Red Oak (*Q. rubra*), Maples (*Acer spp.*), Hickories (*Carya spp.*), and White Oak (*Q. alba*) with nine other species, such as Tulip Poplar (*Liriodendron tulipfera*), used less frequently. However, these data were qualitative and did not examine availability of tree species. Gabbe et al. (2002) investigated tree species use versus availability in southern Illinois and found Cerulean Warblers to be highly selective of hickory species while avoiding others, such as tulip poplar. Lepidoptera larva, an important prey item for Cerulean Warblers, varies by tree species (Holmes and Schultz 1988); this variation could result, potentially, in tree species selectivity. Gleaning insects from leaves appears to be the primary method of food acquisition (Hamel 2000b). Hamel (2000b) describes typical foraging microhabitat locations being in the canopy near dense clusters of leaves where Cerulean Warblers navigate along tree branches looking at upper and lower leaf surfaces. In general, however, Hamel (2000b) identified foraging habitat and ecology as a priority research topic.

Cerulean Warbler population response to silvicultural treatments could provide vital habitat use and conservation information. Few studies have examined response of Cerulean Warblers to silvicultural treatments (Wood et al. 2005). No studies have investigated the effects of silvicultural treatments, and the associated change in forest structure and composition on Cerulean Warbler foraging behavior, yet timber harvesting is a substantial portion of the economy in the core range of the species (Childs 2005). This study examined the response of Cerulean Warblers to silvicultural practices resulting in varying degrees of habitat disturbance in relation to their foraging resource requirements within their core breeding range (Figure 1).

LITERATURE REVIEW

FORAGING ECOLOGY AND HABITAT USE AND SELECTION

Cerulean Warbler.-- Cerulean Warblers are a small, insectivorous, Neotropical migrant that breeds in mature deciduous forests of eastern North America and winters along the Andean montane subtropical forests of northern South America (Hamel 2000b). Basic, yet vital, information on the biology and ecology of the Cerulean Warbler needs to be gathered with respect to their entire annual cycle including breeding, stopover, and wintering habitat (Rappole 1995, Hamel 2000b). Currently, evidence suggests that Cerulean Warbler populations are declining as a result of habitat loss or degradation on the breeding and wintering grounds (Hamel 2000b). Significant loss of appropriate habitat during any part of their annual cycle can result in a decrease in Cerulean Warbler populations (Rappole 1995, Sherry and Holmes 1995). Steep declines in populations resulted in a petition, in 2006, to the U.S. Department of the Interior, Fish and Wildlife Service (USFWS) requesting that the Cerulean Warbler be listed as "threatened" under the Endangered Species Act of 1973 (Hamel et al. 2004). The USFWS ruled that listing of Cerulean Warblers was not warranted because the species will not be endangered in all of, or a

significant part of, its range within the foreseeable future even with the assumption that the rate of decline (-4.1% per year) remained constant.

Loss of mid-elevation montane forests in the Andes Mountains is greater than any other forested habitat type in that region (Robbins et al. 1992). Cerulean Warblers do use shade grown coffee plantations, survival comparisons are needed between plantations and interior forest (Jones et al. 2000). Survival estimates suggest that events on wintering grounds are responsible for most adult male mortality and that current reproductive fitness is not adequate to offset adult mortality (Jones et al. 2004). Habitat loss along migratory stopover locations also could be important but information pertaining to the migratory period is lacking with one exception from the Mayan Mountains of Belize (Parker 1994). Parker (1994) observed large numbers of Cerulean Warblers along the lower montane forests in early April suggesting that such habitat could be important migratory staging areas.

On the breeding grounds, Cerulean Warblers also are facing habitat loss. Historically, Cerulean Warblers were primarily associated with mature floodplain forest (Hamel 2000b). This habitat type experienced substantial losses as floodplain forests have largely been converted to farmland; currently mature mesic upland forests are selected (Hamel 2000b). Amidst the species' overall decline, there has been some range expansion into Ontario. This, in part, could be due to abandoned farmland succeeding into mature forests (Oliarnyk and Robertson 1996). Veit et al. (2005) compared individuals from areas of population expansion with those from declining populations to quantify variation in microsatellite loci. Based on their work, the Cerulean Warbler population decline does not appear to have affected genetic variation within the species.

Habitat use and selection.-- Habitat use and selection have important ramifications for survival of a species because both influences reproductive and mortality rates (Petit et al. 1995). The evolutionary significance of habitat selection is reflected in the close association between

habitat use and morphology, behavior, and life history traits of a species (Cody 1985). An understanding of habitat use and ecological requirements thus forms the framework for conservation efforts of all species (Cody 1985, Probst and Crow 1991).

The study of habitat selection has received considerable attention (Jones 2001). Morse (1985) explains that habitat structure could be essential to habitat selection and that sensitivity to habitat variation differs among warbler species. Habitat models have been created to explain patterns in species abundance and distribution (MacArthur and Pianka 1966, Rosenzweig 1991). Habitat selection can be influenced by landscape structure (Odum 1950, Karr and Freemark 1983, Holmes et al. 1986, Greenberg et al. 1995, and Petit and Petit 1996). Hunt (1998) found that the pattern of habitat succession in Vermont and New Hampshire resulted in more mature forest and less early successional habitat which affected American Redstart (*Setophaga ruticilla*) populations.

Cerulean Warblers prefer mature deciduous forests with a diverse canopy structure including tall, large diameter trees with an open understory (Hamel 2000b). Cerulean Warbler population densities are positively associated with large amounts of mature deciduous forest in the landscape (Bosworth 2003). Large populations occur in floodplain forests as well as a variety of mesic uplands (Lynch 1981, Hamel 2000b, Rosenberg et al. 2000). Habitat selection could be opportunistic, where individuals select the most mature forests available in that region (Hamel 2000a). Generally, territories include large trees that create dense foliage and high canopies (Jones and Robertson 2001). Jones et al. (2001) found that the species exhibits a degree of habitat plasticity in response to natural habitat disturbance. The species is known to select second-growth forests while being sensitive to forest fragmentation (Oliarnyk and Robertson 1996). Weakland and Wood (2005) found territory density to be greater in intact forest compared to fragmented forests. Perkins (2006) determined gaps to be important in Cerulean

Warbler territory selection, although Barg et al. (2005) found no consistent correlation between core use areas and location of canopy gaps.

Morphological foraging adaptations and patchy distribution of resources might result in a foraging preference for certain tree species in various songbirds (Holmes and Robinson 1981, Parrish 1995a, b). Foraging habitat use and selection has not been thoroughly evaluated for Cerulean Warblers. Gabbe et al. (2002) quantified tree species use by thirteen foraging insectivorous passerines in southern Illinois. Most species foraged in tree species disproportional to availability. Yellow-throated Warblers (*Dendroica dominica*) and the Cerulean Warblers were the most selective. Although Cerulean Warblers exhibited a strong preference towards hickory trees in Illinois, this may not be representative over the entire Cerulean Warbler range and, therefore, additional investigation is warranted.

Response to silviculture.—Response of avian abundance, distributions, and overall reproductive fitness to variability in forest structure is lacking (Marzluff et al. 2000). Forest vegetation structure is an important and well known component of avian habitat selection (MacArthur and MacArthur 1961, Cody 1968, Brown 1992, Petit and Petit 1996, Jones 2001). Forests are dynamic systems with varying micro-habitat characteristics associated with different stages of succession. Selection of suitable habitat is often tied to these different stages of succession (Hunt 1998). Silvicultural practices can imitate natural disturbance regimes and create a more diverse habitat mosaic (Greenberg et al. 1995). Understanding that some species prefer certain stages of forest succession allows forest management to be tailored to meet the habitat requirements of particular species (Probst and Weinrich 1993). Warbler abundance can vary by species to the different silvicultural practices (Freedman et al. 1981, Duguay et al. 2001, McDermott 2007, McDermott and Wood 2008). Franzreb (1983), comparing logged and natural environments, found habitat alteration influenced tree species selection and foraging height of birds in Arizona. Tree species selection by avifauna varied due to modifications of availability

resulting from selective tree species removal. Aspen was not removed from the logged areas and use increased from 5% to 53%. In harvested areas, the canopy was removed completely resulting in overall decreased foraging height.

Hamel (2000b) suggested that managed forests with diverse vertical forest structure due to implementation of selective harvests have canopy gaps that might increase the occurrence of suitable breeding habitat for Cerulean Warblers. Wood et al. (2005) suggested that lack of a diverse vertical forest structure from regenerating clearcuts resulted in lower use by Cerulean Warblers than regenerating harvests with residual canopy trees.

There is some concern that silvicultural practices could result in a decrease in songbird survival rates due to increased nest predation and Brown-headed Cowbird (*Molothrus ater*) parasitism (Paton 1994, Brittingham and Temple 1996). In heavily forested landscapes, however, Brown-headed Cowbird parasitism is less common than in forest tracts located in more agricultural areas (Duguay et al. 2001).

The effects of forest management on avian ecology and conservation contain gaps of understanding and implementation (Thompson et al. 2000). Timber production is a primary land use in West Virginia. If implemented with a conservation objective, a forest management treatment, such as a selective cut, could theoretically mimic tree fall gaps that appear to be preferred by Cerulean Warblers (Oliarnyk and Robertson 1996, Hamel et al. 2004). However, there has not been an empirical study specifically examining Cerulean Warbler response to silvicultural practices. Information gaps in the scientific literature can be addressed based on carefully designed observational studies followed by manipulative experiments (Thompson et al. 2000). This information can then be analyzed for causation rendering it more valuable to the formation of functional management recommendations (Sallabanks et al. 2000).

Mature forest stands often are retained adjacent to harvest areas resulting in a diverse habitat mosaic. Many Neotropical migrants have a negative association with forest openings

while others show either indifference or respond positively (Morse 1985, Thompson et al. 2000, Germaine et al. 1997). Different silvicultural treatments influence invertebrate distributions, the major food source for Neotropical migratory birds (Summerville and Crist 2002, Duguay et al. 2000). This could have important ramifications considering that Lepidoptera are the most common and diverse group of invertebrates in eastern deciduous forests (Hammond and Miller 1998, Summerville et al. 1999). Kilgo (2005) found a decrease in arthropod abundance and Hooded Warbler foraging rate from forest edge to interior forest (defined as >100m). Kilgo (2005) concluded that Hooded Warblers encountered less prey, and therefore, foraged less proficiently near group-selection harvest gaps. These influences could be compounded further by many characteristics of invertebrates (i.e., stage of life cycle, activity level, and cryptic coloration) that can influence rate of selection by foraging individuals (Royama 1970, Cooper and Whitmore 1990, Majer et al. 1990).

Increased primary productivity associated with increased light levels found in canopy gaps might result in increased food availability (Fogden 1972). A warmer microclimate associated with increased light levels can result in increased abundance and activity of flying insects (Blake and Hoppes 1986, Smith and Dallman 1996, Gorham et al. 2002). Additionally, nitrogen is an important limiting factor in growth of invertebrate herbivores (Mattson 1980, Scriber and Slansky 1981, Mattson et al. 1991, Fortin and Mauffette 2002). Increased light levels are correlated with increased levels of nitrogen within leaves (Hemming and Lindroth 1995, Fortin and Mauffette 2002) potentially resulting in an increase in food availability for foraging birds.

Methodology.—We collected two single-point foraging observations. The idea of a second observation being compared to the first to quantify differential rates of visibility among tree species is lacking in the foraging literature. A similar argument was made to ignore the first

foraging maneuver observed while analyzing the second and subsequent maneuvers to reduce bias (Hejl et al. 1990) so applying similar reasoning to substrate selection is, perhaps, relevant.

Research was conducted in 2006 and 2007 at two study sites in West Virginia and one in Kentucky. Additionally, in 2007, data were collected at a study site in Ohio and an additional study site in West Virginia. Study sites included the Lewis Wetzel Wildlife Management Area (LWWMA) in Wetzel County, West Virginia, forested private timberlands in Wyoming County, West Virginia (Wagner), Monongahela National Forest (MON) in Randolph County, West Virginia, Daniel Boone National Forest (DBNF) in Bath and Menifee counties, Kentucky, and the Raccoon Ecological Management Area (REMA) in Vinton County, Ohio (Figure 1). All study sites are within the core of the species range (Hamel 2000).

Four, 20 ha, plots were placed along ridge-tops on northern and eastern aspects at each site. Each plot was generally rectangle shaped and had two, 5 ha, uncut buffers located on the plot ends and a central 10 ha block that received a timber harvest treatment. The treatment area was randomly assigned one of four timber harvesting treatments including an unharvested control, a light treatment similar to a single tree selection harvest (Figure 2), an intermediate treatment approximating a shelterwood harvest (Figure 3), and a heavy treatment approximating a deferment harvest (Figure 4). Respective residual basal area (RBA) per treatment type was 14.5 – 24.3 m^2/ha, 11.5 – 17.1 m^2/ha, and 3.0-9.6 m^2/ha. The treatment mosaic resulted in three, 10 ha segments receiving a timber harvest and a combined 50 ha of uncut forest at each site. Timber harvests were implemented in fall and winter of 2006.

Because of the concurrent silvicultural study, we are presented with an opportunity to quantify response of Neotropical migratory songbirds to typical silvicultural treatments. In addition to the Cerulean Warbler, foraging observations were recorded for Hooded Warbler (*Wilsonia pusilla*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Red-eyed Vireo (*Vireo olivaceus*), and Scarlet Tanager (*Piranga olivacea*).

Objectives

The purpose of this research was to examine foraging behaviors and foraging habitat use versus availability of Cerulean Warblers during the breeding season. Information on tree species preference, foraging height, and temporal variation will assist in quantifying some of the basic ecological information that is lacking, but necessary, for sound habitat management. Specificly I examined if:

1) Cerulean Warblers select tree species proportional to availability.

2) selection of foraging substrate or behavior of Cerulean Warblers are influenced by silvicultural practices.

3) following foraging individuals to an additional tree reduces substrate bias in foraging observations.

4) silvicultural practices influence patterns of Neotropical migratory songbird habitat selection and foraging behavior.

Overview of Chapters

This dissertation has been written in the form of 4 chapters. The first chapter provides the introduction, literature review, research justifications, and project objectives. The second chapter covers the foraging ecology of Cerulean Warblers. The third chapter covers the foraging ecology of the additional five species for which foraging observations were collected. The last chapter covers the attempt to identify observer bias in avian foraging observation based research projects. The last three chapters are written in the style of a targeted scientific journal and will be submitted to the following journals.

Chapter 2- *Conservation Biology*

Chapter 3- *Wilson Journal of Ornithology*

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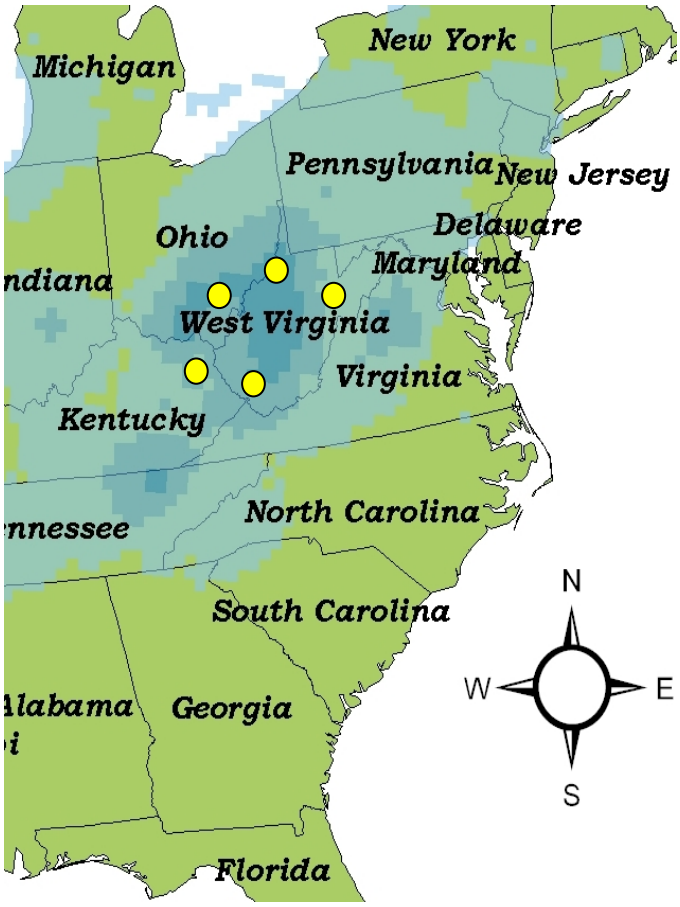

Figure 1: Study area locations in West Virginia, Ohio, and Kentucky. Blue areas represent breeding range, dark blue is the core range, based on Breeding Bird Survey data (Sauer at al. 2008).

Figure 2: Light treatment harvest (residual basal area of 14.5 – 24.3 m^2/ha) at Lewis-Wetzel study area in West Virginia (Photo Credit: Patrick McElhone).

Figure 3: Intermediate treatment harvest (residual basal area of 11.5 – 17.1 m^2/ha) at Lewis-Wetzel study area in West Virginia (Photo Credit: Gregory George).

Figure 4: Heavy treatment harvest (residual basal area of 3.0-9.6 m^2/ha) at Wyoming County study area in West Virginia (Photo Credit: Gregory George).

CHAPTER 2

Influence of silviculture on male Cerulean Warbler (*Dendroica cerulean*) foraging ecology and tree species selection.

Abstract

Understanding foraging ecology provides insight into species resource requirements and overall conservation needs. We examined foraging behavior and tree species selection of male Cerulean Warblers (*Dendroica cerulea*), a species of conservation concern, in response to varying degrees of habitat disturbance from silvicultural treatments at four study sites in West Virginia, Kentucky and Ohio, during the 2006 and 2007 breeding seasons. During 673 foraging observations, Cerulean Warblers foraged primarily in the forest canopy, along branch tips by gleaning insects off leaf surfaces, often adjacent to canopy gaps, both pre- and post-harvest. Aerial foraging increased after harvests. Tree species availability, based on importance values (IV) calculated from density, frequency and basal areas, differed from tree species used for foraging both pre- and post-harvest ($p<0.01$). Preferred species included hickory (*Carya* spp.), sugar maple (*Acer saccharum*), and chestnut oak (*Quercus prinus*), while red oak (*Quercus rubra*) was strongly avoided. Tree species selection changed little post-harvest in all silvicultural treatments. Cerulean Warblers exhibited selection preferences, therefore, maintaining availability of preferred tree species is important for management of Cerulean Warbler populations.

Keywords: Cerulean Warbler, Dendroica, foraging ecology, silviculture

Information on Cerulean Warbler (*Dendroica cerulea*) foraging ecology is limited. Yet, understanding foraging behavior can provide insight into the species ecology, their resource requirements, and overall conservation needs (Petit et al. 1995, Hamel 2000). Hamel (2000) described typical foraging microhabitat locations in the canopy near dense clusters of leaves where Cerulean Warblers navigate along tree branches looking at upper and lower leaf surfaces. Gleaning insects from leaves is the primary method of food acquisition (Hamel 2000). In West Virginia, Cerulean Warblers regularly used multiple tree species for foraging or singing such as chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), maples (*Acer* spp.), hickories (*Carya* spp.), and white oak (*Q. alba*) with nine other species, such as tulip poplar (*Liriodendron tulipfera*), used less frequently (Rosenberg et al. 2000). However, these data were qualitative and did not examine availability of tree species. On the periphery of the species range, Gabbe et al. (2002) investigated tree species use versus availability in southern Illinois and found Cerulean Warblers to be highly selective of hickory species while avoiding others, such as tulip poplar. Abundance of Lepidoptera larva , an important Cerulean Warbler prey item, vary by tree species (Holmes and Schultz 1988, Marshall and Cooper 2004) and microclimate characteristics (Niesenbaum and Kluger 2006); this variation could result in tree species selectivity.

Cerulean Warblers, once common, have declined at a net rate of 4.1% per year from 1966 through 2007 (Sauer et al. 2008). Although they have recently expanded in parts of their range, the species appears to be declining primarily in the core of their breeding range (Jones et al. 2004, Sauer et al. 2008). Consequently, Cerulean Warblers are a focal species for conservation efforts (Hamel et al. 2004). Cerulean Warblers were identified by the U.S. Fish and Wildlife Service (2008) as a bird of conservation concern.

Few studies have examined response of Cerulean Warblers to silvicultural treatments (Wood et al. 2005). No studies have investigated the effects of silvicultural treatments, and the associated change in forest structure, composition, and microclimate, on Cerulean Warbler

foraging microhabitat or behavior, yet timber harvesting is a substantial portion of the economy in the core range of the species (Childs 2005). Cerulean Warbler response to silvicultural treatments, representing varying degrees of habitat disturbance, would provide vital habitat use and conservation information. Specifically, we addressed the following objectives: 1) quantify preferences in foraging habitat and behaviors of Cerulean Warblers in their core range; 2) determine if they forage in association with forest canopy gaps; 3) determine if Cerulean Warblers forage in tree species disproportionately from availability; 4) quantify effects of timber harvesting on foraging habitat, behavior, and tree species selection of Cerulean Warblers.

METHODS

Study area.

Research was conducted in 2006 and 2007 at two study sites in West Virginia and one in Kentucky. Additionally, in 2007, data were collected at a study site in Ohio. Study sites included the Lewis Wetzel Wildlife Management Area (LWWMA) in Wetzel County, West Virginia, forested private timberlands in Wyoming County, West Virginia (Wagner), Daniel Boone National Forest (DBNF) in Bath and Menifee counties, Kentucky, and the Raccoon Ecological Management Area (REMA) in Vinton County, Ohio. All study sites are within the core of the species range (Hamel 2000). In 2006, all sites were predominately mature second growth mixed mesophytic and northern hardwood forests. Predominant tree species at LWWMA and DBNF included maple sp. (*Acer spp*.), oak sp. (*Quercus spp*.), hickory sp. (*Carya spp*.), and tulip poplar (*Liriodendron tulipifera*). Wagner and REMA were similar to LWWMA and DBNF, although maples were a less significant component. Elevation at Wagner was 400-650m, while DBNF, LWWMA, and REMA were between 200-400m. All study areas were characterized by narrow valleys with steep slopes and convoluted ridges with no prevailing orientation.

Four, 20 ha, plots were placed along ridge-tops on northern and eastern aspects at each site. Each plot was generally rectangular shaped with two 5 ha uncut buffers located on the plot ends and a central 10 ha block that received a timber harvest treatment. The treatment area was randomly assigned one of four timber harvesting treatments including an unharvested control, a light treatment similar to a single tree selection harvest, an intermediate treatment approximating a shelterwood harvest, and a heavy treatment approximating a deferment harvest. Respective residual basal area (RBA) per treatment type was 14.5 – 24.3 m^2/ha, 11.5 – 17.1 m^2/ha, and 3.0-9.6 m^2/ha. The treatment mosaic resulted in three, 10 ha segments receiving a timber harvest and a combined 50 ha of uncut forest at each site. Timber harvests were implemented in fall and winter of 2006. Timber selection within harvest areas were independent of tree species resulting in relative stability of tree species composition between seasons. Within the light harvest red oak group increased by 8% while chestnut oak increased by 7% within the intermediate harvest. Although most tree species had a percent change of no greater then +/- 2 percent no other tree species had a greater then 5% change between pre- and post-harvest years.

Surveys

Each 20 ha plot was searched for foraging male Cerulean Warblers between 1 May and 15 July, 2006 and 2007. For each foraging bird located, we recorded a single point observation to avoid statistical issues associated with independence of observations (Hejl et al. 1990). When a foraging bird was first detected, the observer waited 5 seconds before recording any foraging behavior to avoid bias associated with obvious maneuvers (Hejl et al. 1990). Multiple foraging observations per individual per day were recorded with a minimum of 60 minutes between observations. The 60 minute window allows for statistical independence among observations; 1 minute windows have been considered a biologically independent timeframe for Neotropical migrants use of habitat within a territory (Barg et al. 2005).

Data recorded for each observation were foraging maneuver, forest structure, distance from tree bole, adjacency to forest gaps, and tree species occupied. We defined two aerial foraging maneuvers and two near-perch maneuvers similar to Remsen and Robinson (1990). The aerial maneuvers were aerial hawk, the traditional flycatcher maneuver, and sally glean which was used to secure sessile prey on vegetative surfaces. The near-perch maneuvers were vegetation pick, a pick maneuver towards vegetative surfaces and woody picks directed towards branches or tree bark.

Forest structure was recorded as position within the vegetative column and was divided into under-story, mid-story and canopy. Foraging distance from the center, or bole, of the tree was divided into five, 20-percentile, categories starting from the tree bole and moving outward. The first category was the inner most 1-20% of branch length while the last category was the outermost 80-100% of the branch tips. Four categories of canopy gaps were identified: no gap, a small gap similar to a single tree fall gap or single tree removal, an intermediate gap such as a road edge or small tree group removal, or a large canopy gap that resulted in forest clearing such as a wildlife food plot or large tree group removal. A foraging observation was considered adjacent to a gap if the tree occupied was adjacent to the canopy gap.

To quantify availability of forest structure ocular tubes were used to determine presence or absence of vegetation within the understory (0.5-3m), mid-story (3m-12m), and canopy (>12m).

To characterize foraging habitat, behavior, and association with canopy gaps of male Cerulean Warblers, we summarized data from foraging observations across study areas and silvicultural treatment plots for each year to increase sample sizes among treatment areas. Data from all 4 study areas and all 4 treatment plots were included.

To determine whether Cerulean Warblers foraged on trees proportional to availability, we used a 2.5x factor metric prism to quantify tree species availability on the West Virginia and

Kentucky plots. We recorded species of each live tree and DBH (diameter at breast height) of each tree or snag in the prism plot. Locations of prism plots were randomly selected with 20 prism plots per study plot (one per ha). Importance values (IV) were calculated from relative density, relative frequency, and relative basal areas to determine tree species preference (Holmes and Robinson 1981, Gabbe et al. 2002). Importance values were converted into importance percentages to characterize overall tree species availability to foraging individuals. Tree species with IV $\leq$ 2% had too few foraging observations to be included in analyses. Twelve tree species or groups (Figure 1) met the 2% IV criteria. Due to inconsistencies in identification of hickory and oak trees to species, we grouped all hickory and red oak species into their respective single categories of hickory and red oak.

To quantify forest structure availability, ocular tubes were used to determine presence or absence of vegetation within six height classes (0.5-3m, 3-6m, 6-12m, 12-18m, 18m-24m, and >24m) centered on each prism plot. Five ocular determinations were made every 2.3m in each cardinal direction, with an additional center point, totaling 21 ocular determinations within each height class. The six height classes were combined into three forest structure categories, understory (0.5-3m), mid-story (3m-12m), and canopy (>12m). Percent availability was based on the total number of positive ocular determinations for vegetation, out of maximum possible across all study areas, within each height class. Relative percent of forest structure availability was calculated for uncut forest, light harvest, and intermediate harvest.

It is important to view resource availability from the perspective of the forager (Hutto 1990), as much as possible. To verify that trees of all available diameters were used by Cerulean Warblers for foraging, we inspected the distributions of tree diameters at breast height (DBH) for trees available in the 2007 field season (Figure 2), which could influence the interpretation of resource availability. Based on the similarities between DBH distributions for use versus

availability, it appears that Cerulean Warblers selected trees irrespective of their DBH, therefore, no modification of the tree availability dataset was needed prior to analysis.

To compare data pre- and post-harvest, we combined foraging observations across three study areas for analysis. The Ohio dataset was excluded because it did not contain pre-treatment data. Additionally, we excluded foraging observations from the heavy treatment plots because of the extremely small sample size. Unharvested controls and buffer areas were combined into the category, uncut forest, because of low detections in controls.

Statistical Analyses

We compared foraging variables (foraging maneuver, forest structure, distance from tree bole, adjacency to forest gaps, and tree species occupied) between pre-treatment and post-treatment seasons with the Fisher Exact test because some categories had expected values of less than five (Conover 1999). We used paired chi-square tests to discern which foraging categories were different from pre- to post- harvest with $\alpha = 0.01$ for significance to be more conservative while performing multiple tests.

To quantify tree species selection, we compared observed foraging frequencies to expected frequencies (Holmes and Robinson 1981, Gabbe et al. 2002) using a chi-square goodness-of-fit test with Monte Carlo estimates of exact *p* values for probability. Importance values, calculated for each tree species, were multiplied by the total number of observations to obtain the expected frequencies. Preference indices, deviation of observed versus expected values, are used to depict tree species preference or avoidance. We completed a separate analysis for each treatment type (i.e. light harvest, intermediate harvest, and uncut forest) and year.

All analyses were computed within the R statistical language (R Development Core Team, 2007). We set $\alpha = 0.05$ for significance for all tests except paired chi-square tests.

Results

General Foraging Behavior and Habitat

We collected 673 foraging observations of male Cerulean Warblers from four study sites (Table 1). During the 2006 pre-treatment season, they used vegetation picks most often (73.3%) followed by wood-pick (19.3%), sally-glean (6.8%), and aerial hawk (<1%). For the post-treatment season the pattern was similar (65.4%, 12.2%, 17.7% and 4.7% respectively).

During both the 2006 and 2007 breeding seasons, the majority of Cerulean Warbler observations were in the forest canopy (74.7% and 86.2% respectively). The mid-story had 24.0% and 13.0% of foraging detections, respectively, while the understory only accounted for 1.3% and 0.8% of foraging maneuvers in each year. Variation in percent forest structure availability between pre- and post-harvest was minimal (Table 2). In the light harvest, percent change of understory, mid-story, and canopy was -3.3%, 2.1%, and 1.2% respectively and 0.7%, 0.3, and -1.0% respectively for the intermediate harvest.

For distance from bole, the majority of observations were in the outer two distance categories accounting for 26.0% and 42.3% of observations during the pre-treatment year. Post-treatment was similar, 25.8% and 35.5% respectively.

Cerulean Warblers foraged away from canopy gaps during the pre-treatment year 33.4% of the time, but gaps of some form were used on a regular basis (66.6%). Specifically, small gaps were used the most (33.1%) followed by intermediate (25.9%) then large gaps (7.5%). During the post-treatment year, Cerulean Warblers spent the least amount of time foraging away from canopy gaps (19.0%), small gaps were used 24.1%, with intermediate and large gaps being used 31.3% and 25.6% respectively.

Silvicultural Influences on Foraging Behavior and Habitat

Use of foraging maneuvers differed pre- and post-treatment in both harvests but not in uncut forests (Table 3). Cerulean Warblers increased their use of aerial foraging maneuvers (sally-glean and aerial hawk) by a magnitude of three or more in the light and intermediate harvests post-treatment.

Forest structure use in uncut forested areas and the intermediate harvest had a significant decrease in mid-story use between years. No significant change occurred in the light harvest (Table 3).

Cerulean Warblers generally shifted their foraging away from branch tips towards a more moderate distance away from the tree bole in the light and intermediate harvests, although the latter was not statistically significant (Table 3). No significant change occurred in the uncut forested areas (Table 3).

Canopy gaps were important for foraging Cerulean Warblers and use changed pre- and post-treatment in both harvests (Table 3). Between years, in the light harvest, we had an overall decrease in foraging associated with no gap and small gap categories while a ten-fold increase was associated with intermediate gaps and foraging associated with large gaps doubled. In the intermediate harvest, foraging use of all gaps decreased, while use of large gaps had a ten-fold increase (Table 3).

Tree Species Selection

Although only twelve tree species occurred frequently enough to be included in analyses of tree species preference, Cerulean Warblers foraged in 23 different tree species or groups. Across all treatments and study areas, Cerulean Warblers selected tree species disproportionate to availability for both pre-treatment and post-treatment seasons ($p<0.01$ for each season). During both field seasons, they preferred chestnut oak, the hickory group, and sugar maple while

avoiding the red oak group (Figure 1). The remaining 8 tree species, while trending towards slight avoidance, were used relatively proportional to availability.

Comparing pre- and post-harvest years for each harvest treatment, Cerulean Warblers selected tree species disproportionate to availability across all treatment types (Table 4). We generally found positive preference index scores, of varying degrees, for chestnut oak, hickory group, and sugar maple, while red oaks were avoided. Tree species selection was consistent across harvests types indicating overall lack of harvest specific influence.

Overall change in tree species availability, within the harvest areas, was low between seasons (Table 5). Only one tree species per harvest type changed >5%. The red oak group increased 8% in the light harvest and chestnut oak increased 7% in the intermediate harvest.

Discussion

Foraging Behavior

Male Cerulean Warblers primarily foraged in the forest canopy out along branch tips by gleaning insects off leaf surfaces as similarly described by Hamel (2000). Vegetation structure influences how foragers search for, and secure, prey items (Robinson and Holmes 1982) irrespective of efficiency (Stephens and Krebs 1986). The increased use of aerial maneuvers was only associated with the harvested areas. The silvicultural treatments resulted in a more open forest which can result in increased abundance and activity of flying insects (Gorham et al. 2002, Smith and Dallman 1996, Blake and Hoppes 1986). Although flying insects are not the preferred Cerulean Warbler food source (Hamel 2000), the increased space might allow aerial maneuvers to be more plausible, specifically from a spatial perspective.

Foraging theory provides a framework within which to ask questions about foraging behavior and suggests that individuals will respond in a way that will result in a net increase in their reproductive fitness (Stephens and Krebs 1986). The two major decisions a forager has to

make are what prey items to select and at what moment to leave a foraging location, a patch, and travel to a new patch. The forager tries to balance these two decisions and yield the highest net energy gain.

Aerial maneuvers are more energy expensive than near-perch maneuvers and potentially expose the individual to increased predation by making itself more obvious. Considering that the Cerulean Warbler is evolutionarily predisposed to be an efficient near-perch gleaner, morphologically and behaviorally (Cody 1985), the shift in maneuver selection towards aerial maneuvers within the forest treatments might be the outward expression of decreased foraging efficiency within treatment areas compared to individuals foraging within the uncut forest areas. In a study on energy budgets in Dark-eyed Junco (*Junco hyemalis*), birds experiencing a negative energy budget were likely to engage in more risk prone behavior (Caraco 1981). Additionally, birds have been found to exhibit risk prone behavior when in need to increase mass (Bednekoff and Houston 1994).

Association with Canopy Gaps

Cerulean Warblers regularly foraged in close proximity to canopy gaps. Vertical complexity in forest structure is known to be important to the Cerulean Warbler (Lynch 1981, Hunter et al. 2001, Perkins 2006). The increased amount of sunlight in forest gaps results in a more vertically diverse forest structure, either by increased sapling growth or epicormic branching from large trees. Increased diversity of forest structure would be associated more to older canopy gaps that were available during the pre-harvest year, then the harvest related, canopy gaps due to lack of time for harvest response. In addition to foraging, nest site selection (Oliarnyk and Robertson 1996) and placement of territories (Perkins 2006) are often adjacent to canopy gaps. Canopy gaps specifically related to silvicultural activities are used routinely by Cerulean Warblers. Selective harvests in North Carolina (Lynch 1981), two-aged stands in West

Virginia (Nichols 1996), and clearcut stands, 16 years post-harvest, (Wood et al. 2005) each contained Cerulean Warbler populations. Canopy gaps, regardless of disturbance source, appear to be an important component of Cerulean Warbler habitat.

The use of canopy gaps was potentially related to resource availability. Increased primary productivity associated with increased light levels found in canopy gaps might result in increased food availability (Fogden 1972) in the form of Lepidoptera larva. Lepidoptera are the most common and diverse group of invertebrates in eastern deciduous forests (Hammond and Miller 1998, Summerville et al. 1999) and represent an important food source for Cerulean Warblers (Hamel 2000). Additionally, the warmer microclimate associated with increased light levels could result in increased abundance and activity of flying insects (Blake and Hoppes 1986, Smith and Dallman 1996, Gorham et al. 2002) which could help explain the increased use of aerial foraging maneuvers post-harvest when there were more canopy gaps. Nitrogen is known to be an important limiting factor in growth of invertebrate herbivores (Mattson 1980; Scriber and Slansky 1981, Mattson et al. 1991, Fortin and Mauffette 2002). Increased light levels are correlated with increased levels of nitrogen within leaves (Hemming and Lindroth 1995, Fortin and Mauffette 2002) potentially resulting in an increase in food availability for foraging birds. However, Kilgo (2005) found a decrease in foliage-dwelling arthropod abundance from forest edge to interior forest, defined as >100m from the edge, and concluded that Hooded Warblers (*Wilsonia citrine*) encountered less prey, and therefore foraged less proficiently, lower attack rate, near gaps. Different silvicultural treatments influence invertebrate distributions, the major food source for Neotropical migratory birds (Summerville and Crist 2002, Duguay et al. 2000). Heavy harvests had reduced invertebrate species richness (Summerville and Crist 2002) and biomass (Duguay et al. 2000). Summerville and Crist (2002) found no difference in species richness between selectively logged and unlogged stands.

Cerulean Warblers increased their foraging activities adjacent to canopy gaps post-treatment, although this increase was only associated with treatment areas while canopy gap use in uncut forested buffers remained unchanged. Additionally, an overall increase in territory density was observed within treatment areas (unpublished data).

Tree Species Selection

Within the core range of Cerulean Warblers, we observed strong selection of some tree species while others were avoided. Therefore, maintaining availability of preferred tree species, such as hickories, sugar maple, and chestnut oak, may be important for the management of Cerulean Warbler populations. Trends of tree species preference were relatively consistent across silvicultural treatment types in our study. This suggests that some other component, perhaps variability in Lepidoptera larva, might be the catalyst for tree species preferences (Holmes and Schultz 1988).

Red oaks were strongly avoided across treatments and years. This could be due to relatively high tannin levels in red oak leaves (Wood 2005). Additionally, in northern Japan, increase d tannin levels among tree species resulted in reduced Lepidoptera larva biomass (Murakami 1998). Some Lepidoptera larva species are known to have difficulty digesting leaves with higher tannin levels which results in poor growth, and therefore, reduced overall biomass of larva (Karowe 1989).

Marshall and Cooper (2004) determined that abundance of Lepidoptera larva varied during the breeding season within and among tree species. Highest densities of larva were found in the pre-nesting season with lower densities during the breeding season. Marshall and Cooper (2004) found that red oak had comparable Lepidoptera larva abundance to maples, hickories, white oak, and chestnut oak (about 30 caterpillars/ kg leaf biomass). Because red oaks were

avoided for foraging in our study, this suggests other factors, such as tannin levels, influenced tree species preferences.

Conservation Implications

These results have two implications of particular importance for the conservation of Cerulean Warblers. First, Cerulean Warbler association with canopy gaps is well established (Oliarnyk and Robinson 1996, Hamel 2000, Perkins 2006). A mature forest naturally develops small canopy gaps in various ways (tree mortality, wind throw, ice storms) creating the diverse forest structure deemed important to Cerulean Warblers. Within the central Appalachian Mountains, forest canopy disturbance is often created through timber management. Wildlife managers have the ability to mimic the natural environment by prescribing low intensity timber harvest to promote the diverse forest structure associated with Cerulean Warbler foraging habitat.

Second, attention should be placed not only on forest structure but also on the resulting tree species composition produced by timber management. Specifically, for Cerulean Warblers, promote retention of sugar maples in the forest canopy. Silvicultural activities implemented to manage Cerulean Warbler populations can maintain availability of preferred tree species for foraging while promoting overall tree species diversity.

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Table 1: Total number of observations by study site and year for the pre- (2006) and post-treatment (2007) seasons. One year of data was collected at the Ohio site, REMA, during the 2007, post-treatment, season.

Study Site	Pre	Post	Total
Daniel Boone National Forest, KY (DBNF)	76	82	158
Lewis Wetzel Wildlife Management Area, WV (LWWMA)	101	159	260
Wyoming County, WV (Wagner)	135	75	210
Vinton County, OH (REMA)	-	45	45
Total	312	361	673

Table 2: Percent availability of forest structure was proportionately similar between years. Data from two West Virginia and the Kentucky study areas combined.

	Uncut Forest		Light Harvest		Intermediate Harvest	
	Pre	Post	Pre	Post	Pre	Post
Forest Structure						
Understory	26.0	23.2	23.7	20.4	24.0	24.7
Mid-story	37.3	32.2	36.8	38.9	32.9	33.2
Canopy	36.7	44.7	39.6	40.8	43.1	42.1

Table 3: Comparison of foraging variables within uncut forest, light harvest, and intermediate harvest treatments combining the Daniel Boone National Forest, Lewis-Wetzel Wildlife Management Area , and Wagner study sites for the pre- (2006) and post-treatment (2007) seasons. Included are Fisher's exact tests comparing pre- and post-treatment years to discern difference between years by harvest type. Paired chi-square tests were used to discern which foraging categories were different from pre- to post- harvest with $\alpha = 0.01$ for significance. Significant results denoted by asterisk.

	Uncut Forest				Light Harvest				Intermediate Harvest			
	Pre		Post		Pre		Post		Pre		Post	
	n	%	n	%	n	%	n	%	n	%	n	%
Foraging Maneuvers												
Vegatation Pick	106	71.6	91	69.5	50	66.7	62	58.5	62	82.7	51	72.9
Wood-Pick	32	21.6	22	16.8	17	22.7	9	8.5	9	12.0	4	5.7
Sally-glean	9	6.1	15	11.5	7	9.3	29	27.4*	4	5.3	11	15.7
Aerial Hawk	1	0.7	3	2.3	1	1.3	6	5.7	0	0.0	4	5.7
Fisher's Exact Test	P=0.24				P<0.01				P=0.01			
Forest Structure												
Understory	2	1.3	1	0.8	2	2.6	1	1.0	0	0.0	0	0.0
Mid-story	35	23.5	16	12.2*	20	26.7	22	20.8	18	24.0	7	10.0
Canopy	112	75.2	114	87.0*	53	70.7	83	78.3	57	76.0	63	90.0
Fisher's Exact Test	P<0.01				P=0.27				P=0.02			
Distance From Bole												
1-20%	8	5.4	3	2.3	0	0.0	3	2.8	2	2.7	3	4.3
21-40%	22	14.8	12	9.2	9	12.0	10	9.4	10	13.3	8	11.4
41-60%	27	18.1	34	26.0	7	9.3	27	25.5*	11	14.7	13	18.6
61-80%	44	29.5	35	26.7	23	30.7	28	26.4	10	13.3	19	27.1
81-100%	48	32.2	47	35.9	36	48.0	38	35.8	42	56.0	27	38.6
Fisher's Exact Test	P=0.57				P=0.02				P=0.09			
Gap Adjacency												
No Gap	56	40.0	55	42.0	18	25.0	5	4.7*	22	30.6	0	0.0*
Small Gap	43	30.7	46	35.1	44	61.1	28	26.4*	7	9.7	2	2.9
Intermediate Gap	31	22.1	20	15.3	4	5.6	56	52.8*	39	54.2	22	31.4*
Large Gap	10	7.1	10	7.6	6	8.3	17	16.0	4	5.6	46	65.7*
Fisher's Exact Test	P=0.54				P<0.01				P<0.01			

Table 4: Cerulean Warbler tree species preference and avoidance values for uncut forests, light harvest, and intermediate harvests combining the West Virginia and Kentucky study areas for pre- (2006) and post-treatment (2007). Preference and avoidance are indicated by positive and negative values, respectively. Observed versus expected values were compared with chi-square goodness-of-fit test with Monte Carlo estimates for p-values.

	Uncut Forest		Light Harvest		Intermediate Harvest	
Tree Species	Pre	Post	Pre	Post	Pre	Post
American Beech	-3.97	0.07	-0.23	-0.54	-2.85	-2.11
Basswood	-0.77	-4.55	1.63	-1.04	-1.08	-1.14
Black Gum	-0.65	-1.00	0.16	-1.61	-1.12	-0.91
Chestnut Oak	6.72	0.44	-0.09	21.33	5.01	4.36
Cucumber Magnolia	-2.12	-0.36	-2.79	1.30	-2.66	-1.34
Hickory Group[a]	-0.01	0.49	9.82	2.42	8.82	5.72
Red Maple	-7.02	-7.07	-4.11	2.39	7.52	3.62
Red Oak Group[a]	-3.58	-5.43	-3.57	-15.15	-3.62	-7.48
Sugar Maple	18.42	22.83	7.21	6.06	-3.73	3.60
Tulip Poplar	7.02	6.84	4.43	-7.67	-3.51	-1.64
White Ash	-1.91	-3.62	-2.58	-0.42	-2.91	0.17
White Oak	-1.59	4.25	-1.70	-0.73	3.05	6.01
n =	143	135	75	106	75	70
$\chi 2$ =	41.7	44.0	28.8	84.4	42.1	24.9
P =	<0.01	<0.01	<0.01	<0.01	<0.01	0.02

[a] Hickory and red oak categories are comprised of all members of their respective groups due to inconsistency in tree species identification.

Table 5: Tree species availability, based on Importance Values (IV), was generally similar between years within the light and intermediate harvest, represented here by percent change between years. Data from three study areas in West Virginia and Kentucky combined.

	IV Change (%)	
Tree Species	Light	Intermediate
American Beech	-0.3	0.9
Basswood	-0.1	1.2
Black Gum	-1.0	-0.8
Chestnut Oak	-2.8	7.2
Cucumber Magnolia	0.3	1.6
Hickory Group[a]	3.2	1.6
Red Maple	-2.9	3.6
Red Oak Group[a]	8.1	-2.7
Sugar Maple	-1.1	-2.6
Tulip Poplar	1.3	-4.1
White Ash	-4.8	-2.9
White Oak	-3.2	-0.9

[a] Hickory and red oak categories are comprised of all members of their respective groups due to inconsistency in tree species identification.

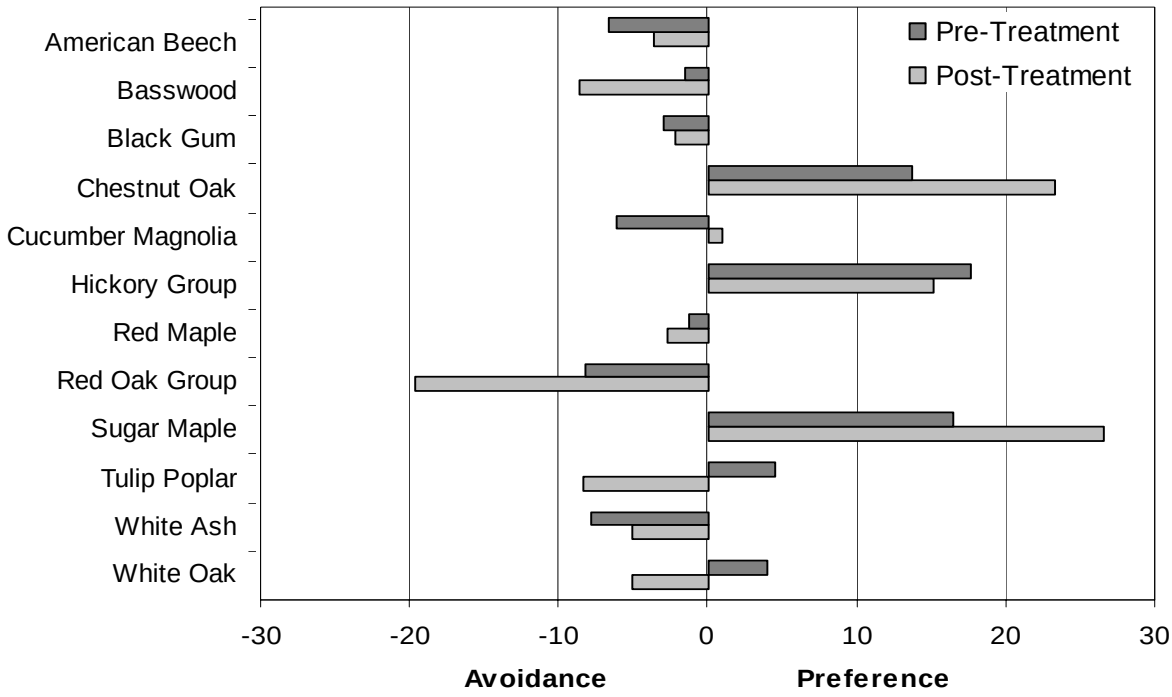

Figure 1: Pre-treatment (2006, n = 312) and post-treatment (2007, n = 316) indices of tree species selection and avoidance for the 12 most available tree species. Indices based on West Virginia and Kentucky study areas combined. Hickory and red oak categories are comprised of all members of their respective groups due to inconsistencies in tree species identification.

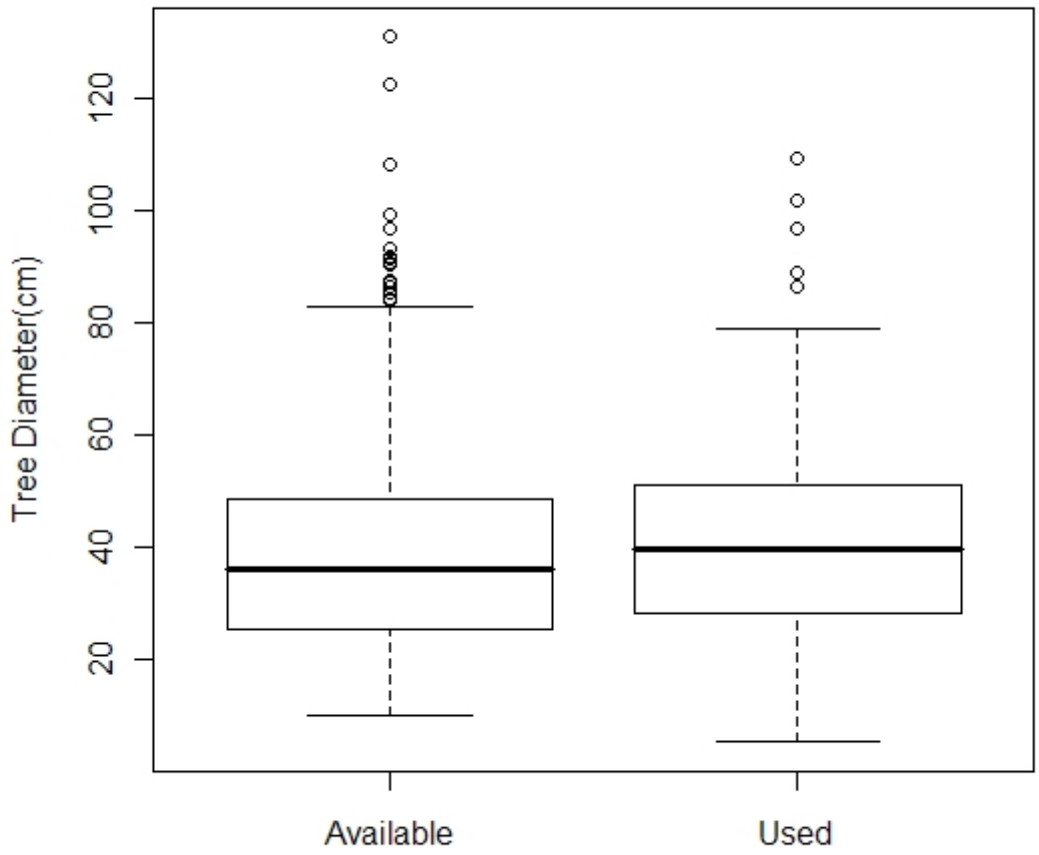

Figure 2: Similarities in tree diameter at breast height (DBH) use (n = 315) compared to availability (n = 1855) indicate that Cerulean Warblers select trees irrespective of diameter based on boxplots depicting each samples five-number summary (includes: minimum, maximum, Q1, Q3, and median with outliers depicted as circles).

CHAPTER 3

Foraging ecology and tree species selection of five Neotropical migrants in West Virginia.

Abstract

Species resource requirements are an important component of habitat selection. We investigated foraging ecology and tree species selection of five Neotropical migrant species; American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Hooded Warbler (*Wilsonia citrine*), Red-eyed Vireo (*Vireo olivaceus*), and Scarlet Tanager (*Piranga olivacea*) at three study sites in West Virginia before (2006) and after (2007) habitat disturbance from silvicultural treatments. Tree species availability, based on importance values (IV) calculated from relative density, frequency, and basal area, differed from tree species used for foraging pre and post-harvest ($P < 0.01$). Aerial maneuvers increased post-treatment for all species except Black-and-white Warbler. At the avian guild level, sugar maples (*Acer saccharum*) were preferred while red oaks (*Quercus* spp) were avoided. Tree species selection changed little post-harvest. Red-eyed Vireo and post-harvest American Redstarts exhibited significant tree species selection preferences ($P < 0.05$) while Scarlet Tanagers were near-significant in tree species selection ($P = 0.06$). Understanding habitat use patterns, in response to habitat disturbance, is important for the management and conservation of Neotropical migrant species.

Keywords: foraging ecology, Neotropical Migrant, silviculture, tree species use

Morphological foraging adaptations and patchy distribution of resources might result in a foraging preference for certain tree species as more selective foragers are distributed less evenly across the landscape (Holmes and Robinson 1981, Parrish 1995a, b). The study of habitat selection has received considerable attention (Jones 2001). Habitat structure could be essential to habitat selection (Morse 1985, Conner and Dickson 1997), and habitat models exist to explain patterns in species abundance and distribution (MacArthur and Pianka 1966, Rosenzweig 1991). However, more thorough evaluation of avian foraging habitat selection and an understanding of avian community-level response is needed. Only two studies quantified selection of tree species for foraging while accounting for relative density, relative frequency, and relative basal area. Gabbe et al. (2002) quantified tree species use by thirteen foraging insectivorous passerines in southern Illinois finding that most species foraged in tree species disproportionate from availability. Similarly, Holmes and Robinson (1981) found that ten focal species they studied in New Hampshire foraged in tree species disproportionate from availability.

Understanding the influence that variability in forest structure has on avian abundance, distribution, and reproductive fitness has conservation implications for forest management (Marzluff et al. 2000). Forest vegetation structure is an important and well known component of avian habitat selection (MacArthur and MacArthur 1961, Cody 1968, Franzreb 1983, Brown 1992, Petit and Petit 1996, Jones 2001). Selection of suitable habitat is often tied to different stages of succession (Freedman et al. 1981, Hunt 1998), and silvicultural practices can imitate natural disturbance regimes by creating a more diverse habitat mosaic (Greenberg et al. 1995), which is an important consideration for habitat management (Probst and Weinrich 1993). Neotropical migrants have a range of responses to forest openings which are not fully understood (Morse 1985, Thompson et al. 1992, Thompson et al. 2000, Germaine et al. 1997). Silvicultural

treatments can influence invertebrate distributions (Duguay et al. 2000, Summerville and Crist 2002), which is important considering that Lepidoptera are an important food source for Neotropical migratory passerines.

Understanding foraging habitat selection and the avian community response to changes in habitat structure influences Neotropical migrant conservation. In this paper we present foraging data for five Neotropical migrants: American Redstart, Black-and-white Warbler, Hooded Warbler, Red-eyed Vireo, and Scarlet Tanager. The specific objectives were to determine if each species' foraging behaviors were influenced by silvicultural practices and determine if any species select tree species disproportionately from availability. Tree species selection has received little attention and is of particular importancefor foraging substrate selection because it is directly related to acquiring adequate food resources. We studied the interaction between foraging ecology and substrate use under the influence of silvicultural practices to help guide management activities associated with silviculture in the central Appalachians. Out results are compared to the literature on foraging tree species selection to discern whether broad patterns exist.

Methods

Study area.

Research was conducted in 2006 and 2007 at three study sites in West Virginia. Study sites were located on the Lewis Wetzel Wildlife Management Area (LWWMA) in Wetzel County, forested private timberlands in Wyoming County (WYO), and the Monongahela National Forest (MON) in Randolph County. In 2006, all sites were primarily mature, second-growth, mixed mesophytic and northern hardwood forests. Predominant tree species at LWWMA and MON include maple

sp. (*Acer* spp.), oak sp. (*Quercus* spp.), hickory sp. (*Carya* spp.), and tulip poplar (*Liriodendron tulipifera*). The WYO study site had similar predominant tree species although maples were a less significant component. Elevation at WYO was 550 - 650m, LWWMA was 300 - 400m, and MON was 650 - 800m. LWWMA and WYO study areas were characterized by narrow valleys with steep slopes and convoluted ridges with no prevailing orientation. The MON site is part of the Ridge and Valley Province where ridge orientation is northeast to southwest.

Four, 20 ha, plots were placed along ridge-tops on northern and eastern aspects at each site. Each plot was generally rectangular and had two, 5 ha uncut buffers located on the plot ends and a central 10 ha treatment block. The treatment area was randomly assigned one of four timber harvesting treatments including an unharvested control, a light treatment similar to a single tree selection harvest, an intermediate treatment approximating a shelterwood harvest, and a heavy treatment approximating a deferment harvest. Residual basal area (RBA) for harvest treatment types was 14.5 – 24.3 m^2/ha, 11.5 – 17.1 m^2/ha, and 3.0-9.6 m^2/ha. The treatment mosaic resulted in 3, 10 ha segments receiving a timber harvest and a combined 50 ha of uncut forest at each study site. Timber harvests were implemented through commercial logging in fall and winter of 2006.

Surveys

Each 20 ha plot was searched for five species of foraging Neotropical migrants, several times per week, between 1 May and 15 July, 2006 and 2007. For each foraging bird located, we recorded a single point foraging observation to ensure independence of observations (Hejl et al. 1990). When a foraging bird was first detected, the observer waited 5 seconds before recording any behavior to avoid bias associated with obvious maneuvers (Hejl et al. 1990). Multiple

foraging observations per individual per day were recorded with a minimum of 60 minutes between observations. The 60 minute window allows for statistical independence among observations; 1 minute windows have been considered a biologically independent timeframe for Neotropical migrants (Barg et al. 2005).

Data recorded for each observation were foraging maneuver, forest structure, adjacency to forest gaps, and tree species occupied. We defined two aerial foraging maneuvers and two near-perch maneuvers similar to Remsen and Robinson (1990). The aerial maneuvers were aerial hawk, the traditional flycatcher maneuver, and sally-glean which was used to glean sessile prey from vegetative surfaces. The near-perch maneuvers were vegetation pick, a pick maneuver towards vegetative surfaces, and woody picks directed towards branches or tree bark. Due to difficulty in determining sex for Black-and-white Warblers and Red-eyed Vireo in addition to subtle sex determination issues with second-year male American Redstarts and some female Hooded Warblers having black caps all data was not separated out by sex.

Forest structure was recorded as position within the vegetative column and was divided into under-story, mid-story, and canopy. Three categories of canopy gaps were identified: no gap, a small gap similar to a single tree fall gap or single tree removal, and large gap such as a road, tree group removal, or a wildlife food plot. For the 5 focal species, we combined data from foraging observations across study areas and silvicultural treatment plots for each year by species.

To determine whether the target species foraged on trees proportional to availability, we used a 2.5-factor metric prism to quantify tree species availability. We recorded species of each live tree and DBH (diameter at breast height) of each tree or snag in the prism plot. Locations of prism plots were randomly selected with 20 prism plots per study plot (one per ha). Importance values

(IV) for each tree species were then calculated from relative density, relative frequency, and relative basal areas to determine tree species preference (Holmes and Robinson 1981, Gabbe et al. 2002). Importance values were converted into importance percentages to characterize overall tree species availability to foraging individuals. Tree species with IV ≤ 2% had too few foraging observations to be included in analyses. Due to inconsistencies in identification of some trees to species, we grouped all hickory and red oak species into their respective single categories of hickory and red oak. Twelve tree species or groups met the 2% IV criteria.

To compare data pre- and post-harvest, we combined foraging observations from the LWWMA and WYO study areas for analysis. The MNF dataset was excluded because it did not contain pre-harvest data. We excluded foraging observations from the heavy treatment plot because of the extremely small sample size in this treatment (pre-harvest n = 31, post-harvest n = 17). Data were combined from low and intermediate harvests to increase sample size for the harvested treatment. Previous research on Cerulean Warblers found similar foraging responses to these two harvest treatments (G. George, Chapter 2). Unharvested controls and buffer areas were combined into one category, uncut forest, because few foraging observations occurred in controls.

Statistical Analyses

We compared foraging variables (foraging maneuver, forest structure, adjacency to forest gaps, and tree species occupied) between pre-treatment and post-treatment seasons with the Fisher Exact test because some categories had expected values of less than five (Conover 1999). Paired chi-square tests were used to discern which foraging categories were different from pre-

to post- harvest with $\alpha = 0.01$ for significance to be more conservative while performing multiple tests.

To quantify tree species selection, we compared observed foraging frequencies to expected frequencies (Holmes and Robinson 1981, Gabbe et al. 2002) using a chi-square goodness-of-fit test with Monte Carlo estimates of exact *p*-values for probability. Preference indices, deviation of observed versus expected values, are used to depict tree species preference or avoidance by bird species. We completed a separate analysis for uncut forest and harvest areas for each year and species. Additionally, to assess avian guild-level tree species selection, we analyzed data combined across the five focal species. Importance values, calculated for each tree species, were multiplied by the total number of observations defining the expected frequencies and were compared to observed frequencies. Preference indices, deviation of observed versus expected values, are used to depict tree species preference or avoidance. A comparison of light harvest, intermediate harvest, and uncut forest between years was analyzed for selection of tree species pre- and post harvest based on standardized residual comparison with a paired t-test, (R Development Core Team 2007).

All analyses were computed within the R statistical language (R Development Core Team 2007). We set $\alpha = 0.05$ for significance except for paired chi-square tests.

Results

General Foraging Behavior and Habitat

In both years, Black-and-white Warbler most frequently used wood picks, while American Redstart, Hooded Warbler, Red-eyed Vireo, and Scarlet Tanager primarily used vegetation picks and sally-gleans (Table 1). Red-eyed Vireos used aerial maneuvers similarly

between years while all other species increased their use of aerial maneuvers in the 2007 post-harvest year.

Scarlet Tanagers foraged in the canopy pre- and post-harvest (Table 1). The mid-story was primarily used for foraging by American Redstarts, Black-and-white Warbler, and Hooded Warbler. Although Red-eyed Vireos foraged primarily in the mid-story during the 2006 pre-harvest year, they increased their foraging in the canopy post-harvest (Table1). All target species decreased their use of mid-story post harvest, although American Redstarts, Black-and-white Warblers and Hooded Warblers still used mid-story most often post-harvest (Table 1).

All species foraged adjacent to canopy gaps for > 50% of foraging observations pre-harvest and ≥ 73% post-harvest (Table 1). When comparing no gap, small gap, and large gap, pre-harvest Hooded Warblers and Red-eyed Vireos primarily foraged away from canopy gaps. Scarlet Tanagers most often foraged in association with small forest gaps. Large forest openings were regularly used by all species, particularly post-harvest.

Effects of Silvicultural Treatments

Within uncut forest areas, use of foraging maneuvers did not change from pre- to post-harvest years for any focal species (Table 2). However, within harvested areas, a significant difference occurred for American Redstart ($P = 0.03$) and near-significance was detected for Hooded Warblers ($P = 0.06$). Both species greatly reduced use of vegetation picks and increased use of aerial hawks (Table 2).

In uncut forest areas, we found no significant difference in use of canopy strata for any focal species, pre- to post-harvest years (Table 3). Within harvested areas, three focal species had a significant difference in use of canopy strata between years (Hooded Warbler $P = 0.01$,

Red-eyed Vireo P = 0.04, and Scarlet Tanager P = 0.01). All three species greatly reduced use of the mid-story. Hooded Warblers increased understory use, while both Red-eyed Vireo and Scarlet Tanager increased their foraging in the canopy (Table 3).

Within uncut forest areas, only Hooded Warblers had differences in gap use between pre- and post-harvest years (P = 0.02). They increased their use of small and large canopy gaps (Table 4). Within harvested areas, gap use for all focal species changed significantly from pre- to post-harvest (P < 0.01). Black-and-white Warblers, Hooded Warblers, Red-eyed Vireos, and Scarlet Tanagers all primarily foraged away from canopy gaps during the 2006 pre-harvest year; American Redstarts mostly foraged adjacent to large canopy gaps. All focal species increased use of large canopy gaps post-harvest (Table 4).

Tree Species Selection

Tree species selection based on combined foraging data for all focal avian species on all plots combined (n = 679 foraging observations) was statistically different from availability both years (Table 5). Sugar maples were preferred and red oaks were avoided both seasons, while chestnut oak was preferred pre-treatment and avoided post-treatment. Tulip poplar was avoided pre-treatment, then used in proportion to availability post-treatment. Foraging generally occurred in the remaining tree species proportional to availability (Table 5).

At the guild level, significant selection of tree species was not detected in either the light treatment or intermediate treatment pre-harvest (Table 6) but selection occurred post-harvest in the light harvest with avoidance of the red oak group and preference of sugar maples. In uncut forests, preference occurred in both years with avoidance of the red oak group and preference of sugar maples (Table 6). Additionally, we found no significant change in preference indices of

tree species within the light harvest, intermediate harvest, and uncut forest between years (t = -0.62, P = 0.55; t = -0.07, P = 0.95; and t = -0.41, P = 0.69, respectively).

Some focal species selected tree species disproportionately from availability (Table 7) including pre- and post-harvest Red-eyed Vireos and post-harvest American Redstarts. Scarlet tanagers were near statistical significance both years (P = 0.06 each year). Pre-and post harvest Red-eyed Vireos selected sugar maples but avoided red oak. Post-harvest American Redstarts selected sugar maple and tulip poplar but they avoided red oak and chestnut oak. Scarlet Tanagers selected sugar maple and avoided red oak both years. Additionally, Scarlet Tanagers selected chestnut oak, and avoided tulip poplar pre-treatment but avoided chestnut oak and selected white oak post-harvest.

Discussion

Influence of silvicultural practices on foraging behavior and ecology

Forests are dynamic systems with varying micro-habitat characteristics associated with different stages of succession. Selection of suitable habitat is often tied to these different stages (Hunt 1998). Hunt (1998) found that the pattern of habitat succession in Vermont and New Hampshire resulted in more mature forest and less early successional habitat which negatively affected American Redstart populations. Silvicultural practices can imitate natural disturbance regimes and create a more diverse habitat mosaic (Greenberg et al. 1995). Understanding that some species prefer certain stages of forest succession allows an opportunity for forest management to be tailored to meet the habitat requirements of particular species (Probst and Weinrich 1993). Warbler abundance can vary by species to the different silvicultural practices (Freedman et al. 1981, Duguay et al. 2001, McDermott 2007, McDermott and Wood 2008).

Comparing logged and natural environments (Franzreb 1983) found that tree species use varied between sites due to selective tree species removal; aspen was not removed from the logged areas and its use increased from 5% to 53%. In harvested areas, the canopy was removed resulting in an overall decrease in foraging height (Franzreb 1983).

Many Neotropical migrants have a negative association with forest openings while others show either indifference or respond positively (Morse 1985, Thompson et al. 1992, Germaine et al. 1997). Silvicultural harvests influenced foraging behavior differently among focal species, although generally foraging birds increased their use of aerial maneuvers (Table 2) and of large canopy gaps (Table 4) while decreasing forest mid-story use (Table 3). The use of canopy gaps was potentially related to resource availability. Different silvicultural treatments influence invertebrate distributions, the major food source for Neotropical migratory birds (Summerville and Crist 2002, Duguay et al. 2000). Heavy harvests had reduced invertebrate species richness (Summerville and Crist 2002) and biomass (Duguay et al. 2000). Summerville and Crist (2002) found no difference in species richness between selectively logged and unlogged stands. Ramifications could be important considering that Lepidoptera are the most common and diverse group of invertebrates in eastern deciduous forests (Hammond and Miller 1998).

Post-harvest forest gaps were regularly used for foraging within a habitat mosaic of mature forest and forests with openings. All focal species increased their use of large canopy gaps, which indicates tolerance for larger gaps as suitable foraging locations. Increased primary productivity associated with increased light levels found in canopy gaps might result in increased food availability (Fogden 1972). A warmer microclimate associated with increased light levels can result in increased abundance and activity of flying insects (Blake and Hoppes 1986, Smith and Dallman 1996, Gorham et al. 2002), which could help explain the increased use of aerial

foraging maneuvers post-harvest when there were more canopy gaps. Additionally, nitrogen is known to be an important limiting factor in growth of invertebrate herbivores (Mattson 1980, Scriber and Slansky 1981, Mattson et al. 1991, Fortin and Mauffette 2002). Increased light levels are correlated with increased levels of nitrogen within leaves (Hemming and Lindroth 1995, Fortin and Mauffette 2002) potentially resulting in an increase in food availability for foraging birds. However, Kilgo (2005) found a negative continuum in foliage-dwelling arthropod abundance from forest edge to interior forest, defined as >100m, and concluded that Hooded Warblers encountered less prey, and therefore, foraged less proficiently, lower attack rate, near gaps.

Tree Species Selection

Varying degrees of tree species selectivity, between years, were found among the five focal bird species with a mixture of selective and more generalist species (Table 6). Gabbe et al. (2002) found that most species selected tree species disproportional to their availability with the exception of Yellow-throated Vireo based on foraging observations on thirteen bird species. Holmes and Robinson (1981), investigating ten bird species, found all were selective of tree species. It appears that our focal species were less selective with only two species displaying significant, or near-significant, selection during both years. Therefore, in West Virginia, considerations of tree species composition may be less important component to silviculture for some, but not all, bird species.

Sugar maple was an important tree species for foraging Neotropical migrants in West Virginia. Holmes and Robinson (1981) found sugar maple to be avoided in New Hampshire where yellow birch was strongly preferred while Gabbe et al. (2002) found hickories to be

important on study plots absent of sugar maple. It is important to acknowledge that preferences among migrants could vary by location and might be influenced by local tree species diversity and abundance. Holmes and Robinson (1981) had a less diverse forest and thus a small number of different tree species. Gabbe et al. (2002) had a diverse forest although the tree species composition was different from West Virginia with few similar tree species available between West Virginia and Illinois. Of the 19 tree species considered by Gabbe et al. (2002) only 1, red maple, was represented in our study.

Our study had two avian species in common with Holmes and Robinson (1981) and Gabbe et al. (2002), Red-eyed Vireo and Scarlet Tanager. All three studies found each to be selective of tree species. In New Hampshire, Red-eyed Vireos displayed a slight preference for sugar maple (Holmes and Robinson 1981), in West Virginia they preferred sugar maple although in the absence of sugar maple Gabbe et al. (2002) found they selected sugarberry (*Celtis laevigata*). Red oak was avoided in West Virginia, white ash (*Fraxinus americana*) was avoided in New Hampshire (Holmes and Robinson 1981) and pumpkin ash (*F. profunda*) was avoided in Illinois (Gabbe et al. 2002). West Virginia sites did not have a dominant ash species. Scarlet Tanagers preferred sugar maple in West Virginia, yellow birch (*Betula alleghaniensis*) in New Hampshire (Holmes and Robinson 1981) and cherrybark oak (*Quercus pagoda*) in Illinois (Gabbe et al. 2002). Although Scarlet Tanagers preferred sugar maple in West Virginia it was avoided in New Hampshire as was overcup oak (*Q. lyrata*) and sugarberry in Illinois.

Sugar Maples, the most preferred tree species for foraging in our research, is shade tolerant allowing adequate regeneration from smaller forest openings. Under this scenario, wildlife managers can reduce the size of forest gaps while encouraging the growth of a tree species preferred by foraging birds and a tree of economic importance. Oaks, due to their

economic value, are an important timber tree in the central Appalachian Mountains. Silvicultural practices implemented to regenerate oaks might result in decreased avian foraging efficiency considering oak species, in general, were not preferred for foraging. Consistent avoidance was most obvious with the red oak group (Table 7) possibly due to relatively high tannin levels in red oak leaves (Wood 2005). Variation in tannin levels among tree species influence the distribution of Lepidoptera larva (Murakami 1998). Some Lepidoptera larva species are known to have difficulty digesting leaves with higher tannin levels which results in poor growth, and therefore, reduced overall biomass (Karowe 1989).

Marshall and Cooper (2004) determined that abundance of Lepidoptera larva varied during the breeding season within and among tree species. Highest densities of larva were found in the pre-nesting season with lower densities during the breeding season. Marshall and Cooper (2004) found that red oak had comparable Lepidoptera larva abundance to maples, hickories, white oak, and chestnut oak (about 30 caterpillars/ kg leaf biomass). Because red oaks were avoided for foraging in our study, this suggests other factors, such as tannin levels, influenced tree species preferences.

In West Virginia, we identified Red-eyed Vireo and Scarlet tanager as specialists foraging on selected tree species; in contrast Black-and-white Warbler and Hooded Warbler were generalists. American Redstart were generalists the first year, then specialists the second (Table 5). Understanding if avian species are generalists or specialists is useful for understanding resource requirements and overall conservation needs. The degree of selection associated with tree species use is an indicator of how effectively species can respond to variation in resource availability. A management scenario intended for the more selective species might be the most

effective approach. Generalist species will be less influenced by modifications of tree species availability while meeting the requirements of more selective species.

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Table 1: Total number and percent of observations for each species by foraging variable for all study areas and plots combined. Data are presented for the pre-harvest (2006) and post-harvest (2007) years. Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA).

	AMRE				BAWW				HOWA				REVI				SCTA			
	Pre		Post		Pre		Post		Pre		Post		Pre		Post		Pre		Post	
Variable	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Foraging Maneuvers																				
Vegetation Pick	26	41.3	25	23.6	4	13.3	1	2.0	52	46.8	40	27.8	29	40.3	60	37.5	27	36.5	45	27.3
Wood-Pick	11	17.5	21	19.8	25	83.3	41	83.7	15	13.5	34	23.6	9	12.5	29	18.1	15	20.3	35	21.2
Sally-Glean	22	34.9	40	37.7	1	3.3	3	6.1	40	36.0	54	37.5	34	47.2	60	37.5	29	39.2	67	40.6
Aerial Hawk	4	6.3	20	18.9	0	0.0	4	8.2	4	3.6	16	11.1	0	0.0	11	6.9	3	4.1	18	10.9
Forest Structure																				
Understory	6	9.5	10	9.4	6	20.0	8	16.3	23	20.7	60	41.7	4	5.6	12	7.5	6	8.1	20	12.1
Mid-story	44	69.8	58	54.7	23	76.7	33	67.3	74	66.7	66	45.8	49	68.1	71	44.4	31	41.9	51	30.9
Canopy	13	20.6	38	35.8	1	3.3	8	16.3	14	12.6	18	12.5	19	26.4	77	48.1	37	50.0	94	57.0
Gap Adjacency																				
No Gap	18	28.6	20	18.9	11	36.7	9	18.4	54	48.6	16	11.1	33	45.8	43	26.9	23	31.1	31	18.8
Small Gap	19	30.2	19	17.9	8	26.7	8	16.3	18	16.2	27	18.8	22	30.6	24	15.0	28	37.8	27	16.4
Large Gap	26	41.3	67	63.2	11	36.7	32	65.3	39	35.1	101	70.1	17	23.6	93	58.1	23	31.1	107	64.8

Table 2: Comparison of foraging maneuver use between pre- (2006) and post-harvest (2007) years for uncut forest and harvested area (low and intermediate harvests combined) combining the study sites. Included are P-values for Fisher's exact tests comparing pre- and post-treatment years to discern difference between years by forest or harvest area. Paired chi-square tests were used to discern which foraging categories were different from pre- to post- harvest with $\alpha = 0.01$ for significance. Significant results denoted by asterisk.

	Uncut Forest								Harvest							
	Vegatation Pick		Wood Pick		Sally-Glean		Aerial Hawk		Vegatation Pick		Wood Pick		Sally-Glean		Aerial Hawk	
Species[a]	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
AMRE																
Pre	14	42.4	8	24.2	9	27.3	2	6.1	11	50.0*	2	9.1	8	36.4	1	4.5
Post	8	20.5	12	30.8	11	28.2	8	20.5	8	17.0	6	12.8	24	51.1	9	19.1
	P = 0.14								P = 0.03							
BAWW																
Pre	3	18.8	13	81.3	0	0.0	0	0.0	1	8.3	10	83.3	1	8.3	0	0.0
Post	1	5.6	17	94.4	0	0.0	0	0.0	0	0.0	14	93.3	1	6.7	0	0.0
	P = 0.32								P = 0.71							
HOWA																
Pre	32	46.4	9	13.0	27	39.1	1	1.4	14	45.2	3	9.7	12	38.7	2	6.5
Post	24	43.6	13	23.6	15	27.3	3	5.5	11	19.3	10	17.5	25	43.9	11	19.3
	P = 0.20								P = 0.06							
REVI																
Pre	11	33.3	5	15.2	17	51.5	0	0.0	13	43.3	2	6.7	15	50.0	0	0.0
Post	18	36.0	4	8.0	25	50.0	3	6.0	12	32.4	4	10.8	17	45.9	4	10.8
	P = 0.46								P = 0.28							
SCTA																
Pre	16	35.6	8	17.8	18	40.0	3	6.7	8	36.4	6	27.3	8	36.4	0	0.0
Post	8	17.4	9	19.6	25	54.3	4	8.7	21	41.2	10	19.6	15	29.4	5	9.8
	P = 0.28								P = 0.48							

[a] Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA)

Table 3: Comparison of forest structure use between pre- (2006) and post-harvest (2007) years for uncut forest and harvested area (low and intermediate harvests combined) combining the study sites. Included are P-values for Fisher's exact tests comparing pre- and post-treatment years to discern difference between years by forest or harvest area. Paired chi-square tests were used to discern which foraging categories were different from pre- to post- harvest with $\alpha = 0.01$ for significance. Significant results denoted by asterisk.

	Uncut Forest						Harvest					
	Understory		Mid-story		Canopy		Understory		Mid-story		Canopy	
Species[a]	n	%	n	%	n	%	n	%	n	%	n	%
AMRE												
Pre	3	9.1	23	69.7	7	21.2	1	13.6	14	63.6	5	22.7
Post	3	7.7	23	59.0	13	33.3	2	4.3	28	59.6	17	36.2
	P = 0.50						P = 0.30					
BAWW												
Pre	5	31.3	10	62.5	1	6.3	1	8.3	11	91.7	0	0.0
Post	2	11.1	13	72.7	3	16.7	1	6.7	12	80.0	2	13.3
	P = 0.29						P = 0.74					
HOWA												
Pre	14	20.3	46	66.7	9	13.0	6	19.4*	20	64.5	5	16.1
Post	17	30.9	30	54.5	8	14.5	29	50.9	24	42.1	4	7.0
	P = 0.32						P = 0.01					
REVI												
Pre	1	3.0	23	69.7	9	27.3	3	10.0	19	63.3	8	26.7
Post	5	10.0	26	52.0	19	38.0	1	2.7	16	43.2	20	54.1
	P = 0.22						P = 0.04					
SCTA												
Pre	4	8.9	17	37.8	24	53.3	1	4.5	12	54.5*	9	40.9
Post	2	4.3	14	30.4	30	65.2	8	15.7	10	19.6	33	64.7
	P = 0.43						P = 0.01					

[a] Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA).

Table 4: Comparison of forest gap use between pre- (2006) and post-harvest (2007) years for uncut forest and harvested area (low and intermediate harvests combined) combining the study sites. Included are P-values for Fisher's exact tests comparing pre- and post-treatment years to discern difference between years by forest or harvest area. Paired chi-square tests were used to discern which foraging categories were different from pre- to post- harvest with $\alpha = 0.01$ for significance. Significant results denoted by asterisk.

	Uncut Forest						Harvest					
	No Gap		Small Gap		Large Gap		No Gap		Small Gap		Large Gap	
Species[a]	n	%	n	%	n	%	n	%	n	%	n	%
AMRE												
Pre	7	21.2	12	36.4	14	42.4	8	36.4*	5	22.7	9	40.9*
Post	12	30.8	7	17.9	20	51.3	3	6.4	8	17.0	36	76.6
	P = 0.22						P < 0.01					
BAWW												
Pre	6	37.5	4	25.0	6	37.5	5	41.7	3	25.0	4	33.3*
Post	4	22.2	3	16.7	11	61.1	0	0.0	1	6.7	14	93.3
	P = 0.44						P < 0.01					
HOWA												
Pre	33	47.8*	10	14.5	26	37.7	16	51.6*	4	12.9	11	35.5*
Post	13	23.6	14	25.5	28	50.9	1	1.8	7	12.3	49	86.0
	P = 0.02						P < 0.01					
REVI												
Pre	16	48.5	8	24.2	9	27.3	16	53.5*	7	23.3	7	23.3*
Post	18	36.0	8	16.0	24	48.0	1	2.7	9	24.3	27	73.0
	P = 0.18						P < 0.01					
SCTA												
Pre	13	28.9	18	40.0	14	31.1	10	45.5*	9	40.9	3	13.6*
Post	11	23.9	16	34.8	19	41.3	3	5.9	9	17.6	39	76.5
	P = 0.62						P < 0.01					

[a] Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA).

Table 5: Tree species preference index combining all avian species and plots for the Lewis - Wetzel and Wyoming study sites for the pre- (2006) and post-treatment (2007) seasons.

Tree Species	Pre	Post
American Beech	1.3	7.7
Basswood	-6.3	-0.9
Black Gum	5.5	-0.8
Chestnut Oak	16.3	-22.0
Cucumber Magnolia	-8.7	-2.5
Hickory Group[a]	-0.8	3.6
Red Maple	8.7	-0.3
Red Oak Group[a]	-31.0	-44.2
Sugar Maple	55.0	69.1
Tulip Poplar	-21.7	7.4
White Ash	-3.9	-6.9
White Oak	0.1	5.1
n =	276	356
$\chi 2$ =	60.3	68.0
P =	<0.01	<0.01

[a] Hickory and red oak categories are comprised of all members of their respective groups due to inconsistency in tree species identification.

Table 6: Tree species preference index for each harvest treatment for all avian species and plots for the Lewis-Wetzel and Wyoming study sites for the pre- (2006) and post-treatment (2007) seasons.. Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA). All species were combined for analysis.

	Light Treatment		Intermediate Treatment		Uncut Forest	
Tree Species	Pre	Post	Pre	Post	Pre	Post
American Beech	2.0	2.0	-2.4	1.2	2.2	4.9
Basswood	-1.9	2.3	0.1	-2.0	-0.7	-1.6
Black Gum	1.3	0.7	2.8	-2.0	2.2	0.2
Chestnut Oak	2.4	-3.9	13.2	-2.5	1.5	-12.2
Cucumber Magnolia	-2.6	-3.6	-3.2	-1.3	-2.3	-0.1
Hickory Group[a]	-1.3	-2.6	-0.5	0.6	3.6	3.9
Red Maple	0.7	0.5	1.7	1.3	5.3	-3.4
Red Oak Group[a]	-5.0	-19.1	-6.2	-8.1	-18.6	-19.6
Sugar Maple	9.3	22.1	3.3	8.3	26.8	39.4
Tulip Poplar	-3.6	2.3	-4.9	3.2	-10.4	4.9
White Ash	0.5	1.0	-0.8	-1.1	-2.4	-4.1
White Oak	-0.3	0.3	-0.4	1.9	0.8	1.3
n =	44	76	56	90	176	190
$\chi 2$ =	21.9	38.8	19.0	12.2	27.3	37.5
P =	0.45	<0.01	0.95	0.54	0.01	<0.01

[a] Hickory and red oak categories are comprised of all members of their respective groups due to inconsistency in tree species identification.

Table 7: Tree species preference index for each avian species pre- and post-harvest. Included are Chi-square analysis with Monte Carlo simulated p-values comparing observer and expected frequencies of tree species use by five Neotropical migratory songbirds. Focal species are American Redstart (AMRE), Black-and-white Warbler (BAWW), Hooded Warbler (HOWA), Red-eyed Vireo (REVI), and Scarlet Tanager (SCTA).

	AMRE		BAWW		HOWA		REVI		SCTA	
Tree Species	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
American Beech	-0.59	1.76	-0.66	0.19	0.76	2.48	2.11	2.81	-0.86	0.48
Basswood	0.55	0.52	-1.02	-0.25	-3.98	0.09	-0.90	0.60	-1.86	-1.91
Black Gum	0.06	-0.27	2.19	-0.46	1.06	1.57	2.70	-1.25	-1.26	-0.43
Chestnut Oak	2.41	-11.87	0.42	6.37	0.54	-7.46	5.84	-2.58	3.98	-6.46
Cucumber Magnolia	-1.33	0.71	0.03	-0.82	-4.74	-1.57	-2.76	0.76	-0.72	-1.57
Hickory Group[a]	3.97	-1.11	0.49	-0.64	-6.26	2.64	-2.14	2.11	0.96	0.64
Red Maple	0.34	-0.62	2.06	0.62	7.52	0.56	-0.52	1.53	-2.44	-2.44
Red Oak Group[a]	-7.83	-12.09	-2.68	-3.43	-9.96	-8.96	-7.45	-10.75	-6.30	-8.96
Sugar Maple	5.66	13.74	2.78	1.03	7.14	16.72	16.68	15.92	20.77	21.72
Tulip Poplar	2.21	12.86	-1.66	-0.36	-6.86	-4.64	-10.40	-1.86	-8.25	1.36
White Ash	-1.46	-1.71	-0.61	-0.62	-2.97	-1.92	0.27	-1.67	0.30	-0.92
White Oak	-0.64	-0.94	0.31	0.30	-1.34	-1.18	0.05	1.10	1.08	5.82
n =	49	75	22	30	83	81	59	80	63	90
χ^2 =	12.4	37.3	7.5	6.9	20.1	22.9	32.0	24.8	25.2	24.3
P =	0.98	0.02	0.99	0.99	0.32	0.32	0.02	0.02	0.06	0.06

[a] Hickory and red oak categories are comprised of all members of their respective groups due to inconsistency in tree species identification

CHAPTER 4

Analysis of observer detection bias in avian foraging behavior and tree species use.

Abstract

Foraging ecology studies could be biased due to disparity in initial detection probabilities of foraging birds among tree species or foraging behaviors because it might be easier to detect a foraging bird when it is in certain tree species, lower in the canopy, or using aerial foraging maneuvers. Our study investigated whether the initial foraging observation is biased based on 1521 paired, single-point foraging observations for six species of arboreal foraging Neotropical migrants in two study sites in West Virginia and one in Kentucky in 2006 and 2007. We did not detect a significant difference in tree species used for foraging between the initial and second foraging observation ($P \geq 0.62$). Foraging maneuvers and foraging height generally were not significantly different ($P \geq 0.09$) between the two foraging observations for the six avian species tested. We conclude that the initial detection of foraging birds would not have a major influence on interpretation of foraging substrate or behavioral preferences.

Key Words: foraging, Neotropical migrant, observer bias, study design, substrate selection

Much of the literature on design of avian foraging studies has examined autocorrelation in sequential versus single-point foraging observations (Bell et al. 1990, Hejl et al. 1990, Noon and Block 1990, Recher and Gebski 1990), the two standard methods of quantifying avian foraging behavior (Wagner 1981, Bell et al. 1990, Hejl et al. 1990). With single-point observations, only the initial foraging maneuver is recorded. For sequential observations, individual birds are followed for a variable period of time while recording every foraging maneuver implemented (Bell et al. 1990). The single-point method avoids statistical issues associated with independence among observations (Hejl et al. 1990), although Morrison (1984) determined that this method under represents comparatively rare foraging behaviors. Hejl et al. (1990) found that the degree of concealing cover did not influence whether an individual could be followed from initial to subsequent foraging observations; however, they did not evaluate if visibility bias was associated with the initial versus subsequent detection. It might be easier to detect a bird when it is foraging in certain tree species, lower in the canopy, or using aerial foraging maneuvers, all of which could influence interpretation of avian foraging preferences.

Thus, it is important to understand if initial detection probability introduces bias into studies of foraging ecology. Our study investigated whether the initial foraging observation introduced detection bias for six species of arboreal foraging Neotropical migrants by comparing an initial to a second single-point foraging observation to determine if the initial foraging detection unduly influenced interpretation of tree species selection, foraging maneuver used, or vertical height of the foraging individual. The study of a second observation being compared to the first to quantify differential rates of detection among tree species is lacking in the foraging literature.

METHODS

Study area. We conducted the study in 2006 and 2007 on three study areas including the Lewis Wetzel Wildlife Management Area (LWWMA) in Wetzel County, West Virginia, forested private timberlands in Wyoming County, West Virginia (Wyoming), and the Daniel Boone National Forest (DBNF) in Bath and Menifee counties, Kentucky. In 2006, all three sites were predominantly mature, second-growth mixed, mesophytic and northern hardwood forests. Predominant tree species at LWWMA and DBNF included maple sp. (*Acer sp*.), oak sp. (*Quercus sp*.), hickory sp. (*Carya sp*.), and tulip poplar (*Liriodendron tulipifera*). The Wyoming site had tree species similar to the other study areas, although maples were a less significant component. Elevation at the Wyoming site was 400-650 m, while DBNF and LWWMA were 200-400 m. All three study areas are characterized by narrow valleys with steep slopes and convoluted ridges with no prevailing orientation.

Four, 20 ha plots were placed along ridge-tops on northern and eastern aspects at each site. The central 10 ha of each plot was randomly assigned one of four timber harvesting treatments: an unharvested control, a light treatment similar to a single tree selection harvest, an intermediate treatment approximating a shelterwood harvest, and a heavy treatment approximating a deferment harvest. Timber harvests were implemented in fall and winter of 2006.

Foraging observations. We searched each 20 ha plot for foraging Neotropical migrants between 1 May and 15 July, 2006 and 2007. Focal species on the two West Virginia sites were Cerulean Warbler (*Dendroica cerulea*), Hooded Warbler (*Wilsonia citrine*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Red-eyed Vireo (*Vireo olivaceus*),

and Scarlet Tanager (*Piranga olivacea*). At the Kentucky site, observations were recorded only on the Cerulean Warbler.

For each foraging bird located, we collected two single-point foraging observations. The single-point method was used to avoid statistical issues associated with independence of observations (Hejl et al. 1990). When a foraging bird was first detected, the observer waited 5 seconds before recording data for the first foraging observation to avoid bias associated with obvious maneuvers (Hejl et al. 1990). For the second foraging observation, the observer followed the bird to the next tree it selected. We recorded sex when possible and species of the bird, tree species occupied, height within the canopy, and foraging maneuver implemented.

Multiple foraging observations per individual per day were recorded with a minimum of 60 minutes between observations. The 60 minute window allows for statistical independence among observations; 1 minute windows have been considered a biologically independent timeframe for Neotropical migrants (Barg et al. 2005).

We defined two aerial foraging maneuvers and two near-perch maneuvers similar to Remsen and Robinson (1990). The aerial maneuvers were aerial hawk, the traditional flycatcher maneuver, and sally-glean, which is used to secure sessile prey on vegetative surfaces. The near-perch maneuvers were vegetation pick and woody pick.

Foraging height within the tree was assigned one of five height categories based on % relative height. By using % relative height rather than actual height within the canopy, we accounted for variability of forest structure within and among research locations (Terborgh 1980).

Statistical Analysis. We summed the total number of foraging observations in each tree species for each bird species. Then we compared frequency of tree species used in the first and

second observation with a Generalized Cochran-Mantel-Haenszel test (CMH), similar to a three-dimensional contingency table (Faraway 2006, R Development Core Team 2007), for each West Virginia site. The CMH test allowed us to test for variation in tree species use while accounting for different bird species in a single test (Faraway 2006) reducing our chances of committing a Type I statistical error (Zar 1999). For the Kentucky site, we used contingency χ^2 test of homogeneity (Conover 1999) to compare first and second foraging observations for Cerulean Warblers. Although within-site variation of tree species was reduced by clustering the four plots on each study area, the study areas were distant from each other and tree species availability differed. Therefore, we analyzed study areas separately. Only tree species that were used at least 5 times per year were included in the χ^2 test of homogeneity analysis to avoid a large proportion of zero values (Gabbe et al. 2002).

To compare frequency of foraging maneuver and foraging height between first and second foraging observations, we summed the number of detections for each foraging maneuver and each foraging height category by species, study area, and year for each paired observation. We used the CMH test to compare distribution of observations among the foraging parameters for the first and second observation while accounting for study area in one step to avoid the need to individually test each contingency table by study site (Faraway 2006).

Years were analyzed separately for all tests because timber harvesting altered forest structure. Because our objective was to compare the distribution across tree species and foraging maneuvers for the paired observations not if use of a particular tree species or maneuver differed, we did not follow the overall χ^2 or CMH tests with pair-wise comparisons to separate means. Analyses were completed using the R statistical language (R Development Core Team 2007). We considered differences significant at $\alpha = 0.05$.

RESULTS

We collected 709 paired foraging observations in 2006 and 812 in 2007. Distribution of foraging observations among tree species was not different for the first versus second observation at any study site for either year (Table 1). As an example, Cerulean Warbler use of the six most common trees at LWWMA in 2007 was almost identical for the first and second observation (Fig. 1).

With one exception, distribution of foraging maneuvers used was not significantly different between the two foraging observations (Table 2). Use of foraging maneuvers differed between the paired observations only for the American Redstart in 2007 (Table 2).

Similarly, the distribution of detections among foraging height categories was not significantly different between the two foraging observations with one exception (Table 2). In 2006, Red-eyed Vireo use of foraging height categories differed between the two foraging observations.

DISCUSSION

Because we detected no differences in use of tree species between the paired foraging observations, observer bias in the initial detection of foraging birds did not appear to influence interpretation of foraging substrate preference. Even after timber harvesting, with a more open canopy structure, tree species use during the two foraging observations remained the same. As a result, the first foraging observation appears to be sufficient in quantifying tree species use in foraging birds.

We saw a limited number of statistically significant results in analyses of foraging maneuver and foraging height among paired observations (Table 2). Only two species had significant results and only in one season for each species; potentially due to the underlying influence associated with variation detected among comparatively rare foraging maneuvers and heights for those two species. This is somewhat expected considering Morrison (1984) determined that the single-point method is a poor measure of comparatively rare foraging behaviors.

Hejl et al. (1990) suggested that observers wait 5 seconds before recording any behavior to avoid statistical biases associated with obvious maneuvers recorded in the initial foraging detection. Our results suggest that the initial detection of foraging birds also did not influence the interpretation of foraging substrate use. We encourage continued attempts towards the identification of bias in an effort to supplement the sparse literature on the subject while improving the theoretical foundation of avian foraging ecology.

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Table 1: Within-year variation in tree species selection between the first and second foraging observations for each study site by year.

Study Site	Year	*N*	Df	$M^2/\chi^{2\,a}$	*P*
Daniel Boone NF, KY	2006	133	3	0.6	0.90
	2007	158	4	2.7	0.62
Lewis-Wetzel WMA, WV	2006	537	25	21.3	0.67
	2007	802	20	15.0	0.78
Wyoming, WV	2006	661	20	11.6	0.93
	2007	521	22	16.4	0.80

[a] M^2 = Cochran-Mantel-Haenszel test which accounted for variation among avian species at the two West Virginia sites; χ^2 = Chi-square contingency test at the Kentucky site.

Table 2: Variation in maneuver use and foraging height between paired foraging observations by species and year. The Cochran-Mantel-Haenszel test (M^2) accounted for variation among study sites.

			Foraging Maneuver			Foraging Height		
Year	Species[a]	*N*	df	M^2	*P*	df	M^2	*P*
2006	AMRE	126	3	5.4	0.14	4	2.1	0.71
	BAWW	60	2	1.2	0.55	4	4.6	0.33
	CERW	718	3	6.0	0.11	4	8.7	0.35
	HOWA	222	3	1.1	0.79	4	1.7	0.80
	REVI	144	3	6.5	0.09	4	8.4	0.02
	SCTA	148	3	0.4	0.94	4	6.6	0.34
2007	AMRE	180	3	8.0	0.05	4	2.4	0.66
	BAWW	66	2	2.2	0.33	4	3.2	0.53
	CERW	760	3	6.4	0.09	4	3.7	0.45
	HOWA	234	3	1.6	0.66	4	8.1	0.09
	REVI	180	3	2.2	0.53	4	1.7	0.80
	SCTA	204	3	0.9	0.82	4	2.2	0.93

[a] Cerulean Warbler (CERW), Hooded Warbler (HOWA), American Redstart (AMRE), Black-and-white Warbler (BAWW), Red-eyed Vireo (REVI), Scarlet Tanager (SCTA)

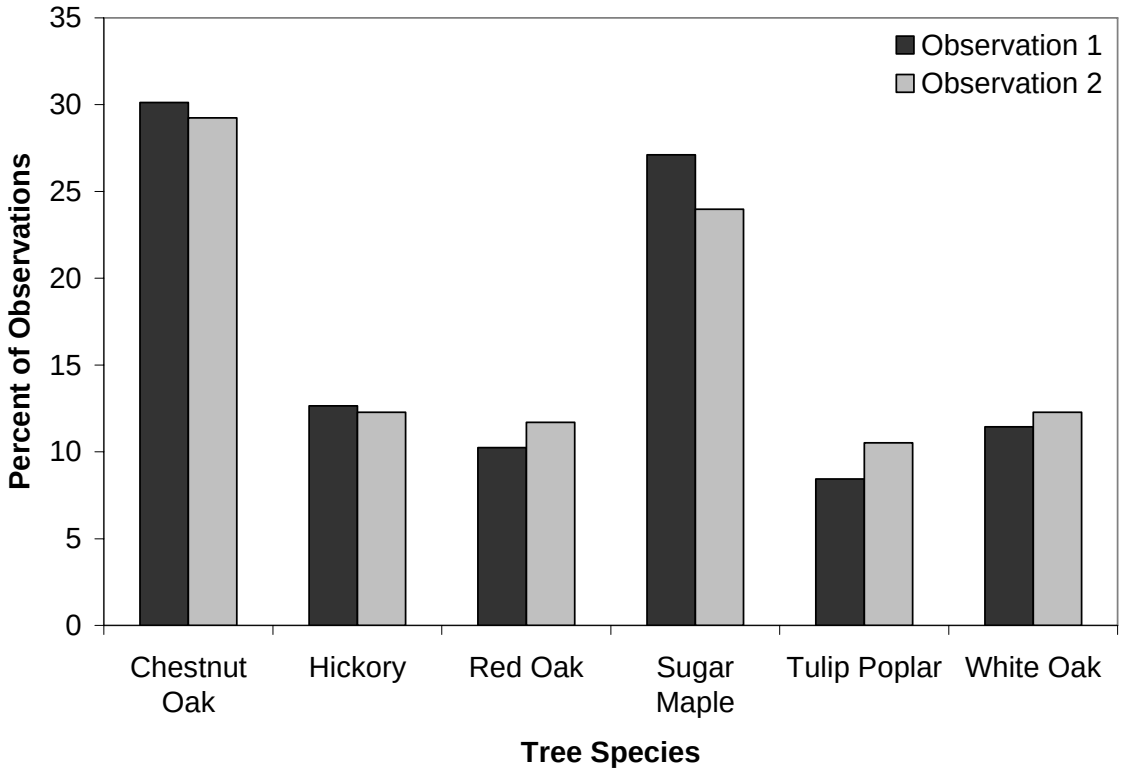

Figure 1: Distribution of Cerulean Warbler foraging observations among tree species at Lewis-Wetzel Wildlife Management Area for 2007. The distribution did not differ for the first versus second observation ($M^2 = 16.4$, $P = 0.80$) at any study site for either year.

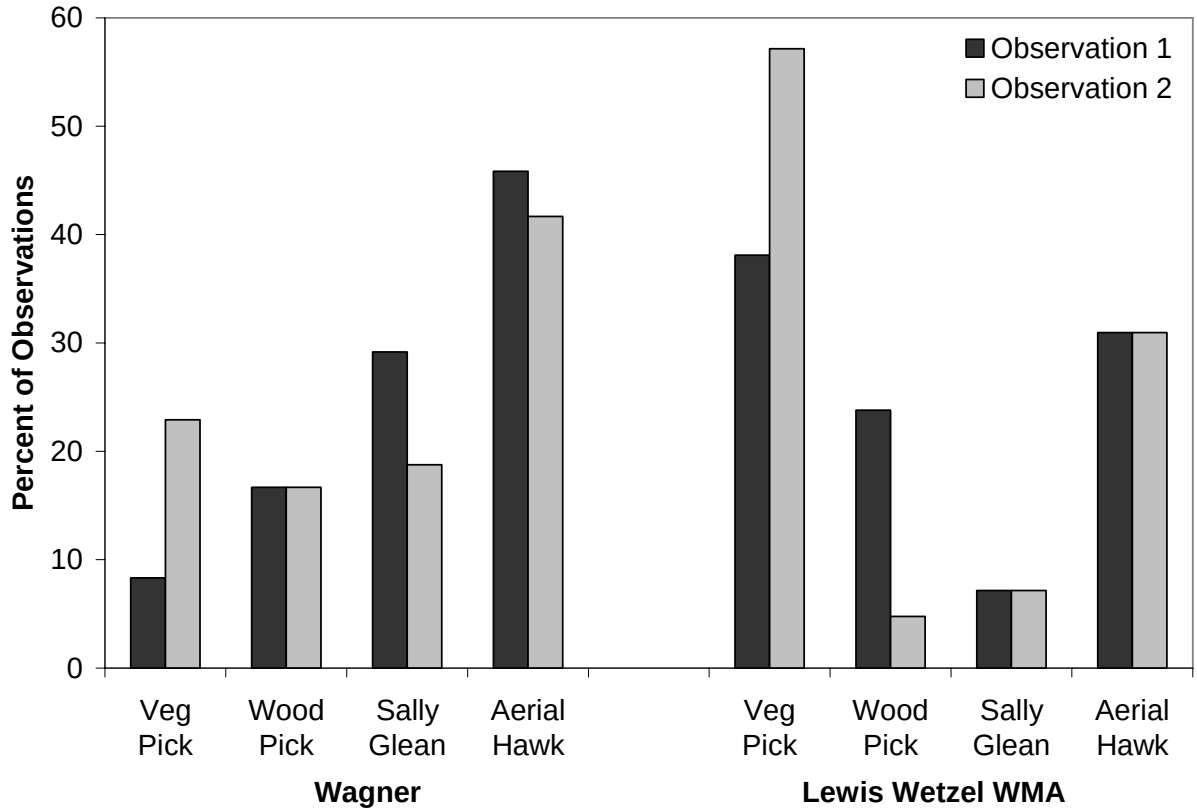

Figure 2: American Redstart use of foraging maneuvers differed between the paired observations in 2007 ($M^2 = 8.0$, $P = 0.05$).